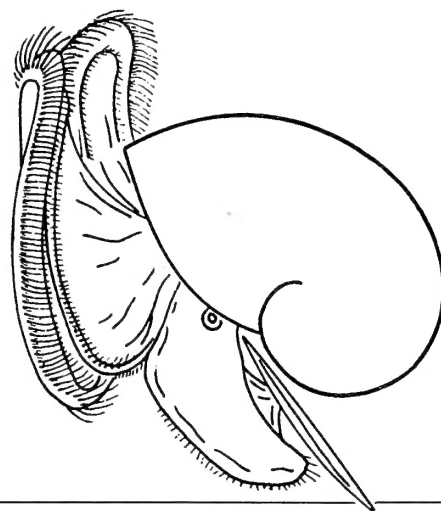


THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 38

January 3, 1995 to October 2, 1995

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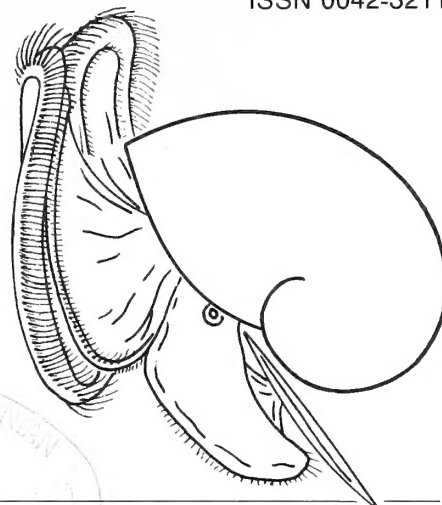
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The Veliger (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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Very short papers, generally not over 750 words, will be published in a "Notes, Information & News" column; in this column will also appear notices of meetings and other items of interest to our members and subscribers.

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Phylogenetic Analysis of 18 Species of Madagascan Acavid Land Snails Using Allozyme Characters

by

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Abstract. Intensive collections employing many local workers achieved unprecedented success in sampling 208 live acavids from 55 populations representing 18 species in three of Madagascar's four acavid genera. Electrophoresis of foot tissues from all of these snails yielded 71 informative characters (alleles and heteropolymers) in 12 loci. No cryptic species were discovered. Phylogenetic analysis of the data yielded a consensus tree suggesting that (a) "*Helicophanta*" *amphibulima* is a species of *Clavator*; (b) *Clavator* is paraphyletic; (c) the remaining *Helicophanta* are paraphyletic and compose an eastern highland clade (*H. betsileoensis*, *H. bicingulata*, *H. ibaraoensis*), an eastern lowland clade with disjunct ecology and conchology (ground-dwelling *H. farafanga*, arboreal *H. souverbiana*), and an isolated western clade (*H. vesicalis*, *H. petiti*); (d) the six species of *Ampelita* form three two-species clades that are diagnosable conchologically but not geographically or ecologically, including *A. (Ampelita) decaryi* (a burrower) and *A. (Eurystyla) julii* (an arboreal); (e) the probable level of synonymy among nominal species is 17%, suggesting about 82 total species on the island; and (f) noteworthy shell convergences include those between "*Helicophanta*" *amphibulima* and *H. farafanga*; *H. petiti* and globose *Ampelita* such as *A. julii*; and *A. sepulchralis* and *A. subfunebris*. Previous predictions that worldwide acavoids will be valuable indicators of ancient Gondwanan tectonic events are supported by these Madagascan taxa, especially *Helicophanta*. Preliminary dissections indicate that many new anatomical characters will contribute to Madagascan and Gondwanan acavoid phylogenetics; taxonomic changes are postponed until such characters can be added at some future date.

INTRODUCTION

This paper is the second in a long-term project to deduce the phylogeny, morphological evolution, and biogeography of the acavoid (= acavid, strophocheilid, megalobulimid, caryodid, etc.) land snails worldwide. These giant, tropical snails are ancient relicts (and valuable biogeographic indicators) of Gondwanaland and are everywhere threatened by deforestation, introduced predators, competition by physiologically harder snails, and exploitation for food (in South America) and money (sale of Madagascan and Sri Lankan shells) (Emberton, in press). The first paper (Emberton, 1990) reviewed acavoids as a well-defined monophyletic clade with an unusually great range of shell shapes both within and among geographical regions; collated all taxonomic and distributional data on the 99 nominal species and four genera of Madagascar; and made a prelim-

inary subgeneric revision of Madagascan acavids based on the limited and admittedly unreliable anatomical data available from the literature. The third paper (Emberton, 1994a) analyzed the estivation sites and external body and shell morphologies of nine diverse acavid species in a phylogenetic context. The fourth paper (Emberton, 1994b) analyzed the distributional patterns of the seven acavid species that occur in the rainforest region of Antalaha, northeastern Madagascar, and compared the results with 20-year-old data from the same region to hypothesize causes for those distributions and to assess the danger of extinction for each species.

Virtually all of the Muséum National d'Histoire Naturelle's anatomical material of Madagascan acavids has been lost, and little existed in any other museums prior to the author's fieldwork in September and October 1990 (Emberton, in press). No Madagascan acavids have ever

Table 1

Electrophoresed samples of Madagascan acavid snails.
ANSP = Academy of Natural Sciences of Philadelphia.

Genus	Species	N	Station	ANSP catalog numbers	
				Alcohol	Dry
<i>Ampelita</i>	<i>decaryi</i>	1	KCE153	A16290	391393
	<i>julii</i>	2	KCE205	A16291	391400
	<i>lamarei</i>	6	KCE204	A16287	391390
		3	KCE205	A16288	391391
		1	KCE237	A16290	391393
		1	KCE238	A16289	391392
		2	KCE252	A16289	—
	<i>sepulchralis</i>	1	KCE156	uncat.	—
		1	KCE158	A16418	—
		13	KCE191	A16419	—
		1	KCE272	A16420	—
	<i>subfunebris</i>	5	KCE164	A16285	391433
		1	KCE158	A16296	—
	<i>xystera</i>	2	KCE161	A16294	391431
		12	KCE206	A16292	391429
		1	KCE297	A16297	—
		8	KCE305	A16293	391430
		1	KCE310	A16294	391431
		1	KCE313	A16299	—
		2	KCE167	A16302	—
<i>Clavator</i>	<i>clavator</i>	6	KCE172	A16301	391438
		1	KCE265	A16305	—
	<i>eximius</i>	1	KCE321	A16306	—
		7	KCE154	A16307	391446
	<i>johnsoni</i>	7	KCE200	A16309	391450
		10	KCE206	A16311	391452
	<i>moreleti</i>	1	KCE250	A16308	391449
		1	KCE210	A16315	391483
<i>Helicophanta</i>	<i>amphibulima</i>	1	KCE249	A16316	391484
	<i>betsileoensis</i>	10	KCE161	A16317	391486
	<i>bicingulata</i>	31	KCE164	A16318	391491
	<i>farafanga</i>	1	KCE164	A16319	391492
	<i>ibaraensis</i>	1	KCE255	A16320	—
		1	KCE262	A16321	—
		1	KCE265	A16323	—
		1	KCE270	A16324	—
		1	KCE271	A16325	—
		1	KCE273	A16326	—
		2	KCE274	A16327	—
		1	KCE279	A16328	—
	<i>petiti</i>	2	KCE189	A16329	391505
		1	KCE158	A16330	391517
	<i>souverbiana</i>	1	KCE159	A16331	391518
		30	KCE161	A16332	391519
		4	KCE164	uncat.	391507
		2	KCE296	A16338	—
		1	KCE297	A16333	391520
		3	KCE300	A16334	391521
		1	KCE302	A16339	—
		3	KCE304	A16335	391522
		1	KCE305	A16336	391523
		1	KCE308	A16340	—
		1	KCE318	A16337	391524
		1	KCE322	A16341	—
	<i>vesicalis</i>	8	KCE172	A16342	391529

been studied biochemically. No phylogenetic analysis of Madagascan acavids has ever been attempted with any more than a few unreliable characters (Emberton, 1990). The difficulties of getting extensive anatomical and frozen-tissue collections result from the ca. 98% deforestation of Madagascar; the inability of acavids (or any other native Madagascan snails) to survive or recolonize after deforestation; the remoteness of most remaining forest patches; the labor-intensity of getting live snails in the dry season; and the general impassability of the "roads" at any time but the dry season (Emberton, 1994a; Bradt, 1992). Fortunately, Malagasy villagers are sometimes available for hire in large numbers as collectors, ameliorating the labor-intensity problem. As an extreme example of how precious some of these samples are, getting the single, first live-collected *Helicophanta farafanga* Adams, 1875, took approximately 90 person-hours of intense search.

The purpose of this paper is a phylogenetic analysis of all the live Madagascan acavids collected in 1990, using allozyme characters. Anatomical investigations have been started but will be delayed for some time due to fieldwork commitments (Emberton, 1994c; in press). Therefore, unlike previous systematics papers by the author that combined anatomical with allozyme data (Emberton, 1988, 1991), only the allozyme data are analyzed here. Taxonomic changes, no matter how strongly warranted, are postponed until the anatomical data can be added.

Allozyme analysis was used instead of preferred DNA sequencing because of the author's difficulties obtaining sequence directly from PCR product (a common problem with land-snail material) and lack of resources for cloning. Despite the shortcomings of allozymes (convergence of alleles in one-dimensional zymograms, unscored alleles due to sampling bias, etc.), allozyme data remain among the easiest and cheapest to obtain for molecular systematics (Richardson et al., 1986; Hillis & Moritz, 1990; Emberton, 1994d). Often a sufficiently large data set can be obtained whereby the informative phylogenetic "signal" is detectable through the homoplastic "noise" (Richardson et al., 1986; Emberton et al., 1990). For phylogenetic analysis (as opposed to population-genetic analysis) of allozyme data, cladistic methods (Hennig, 1966; Wiley, 1981; Brooks & McLennan, 1991; Harvey & Pagel, 1991) are preferred by this author to distance methods or to frequency parsimony (Emberton, 1994d).

MATERIALS AND METHODS

Tissue samples were taken from 208 snails from 55 populations representing three genera and 18 nominal species of Madagascan acavoids. These comprised six species of *Ampelita* Beck, 1837, four species of *Clavator* Martens, 1860, and eight species of *Helicophanta* Férussac, 1821. (No *Leucotaenius* Martens, 1860, were collected in 1990, despite intensive search along the southwestern coast where that genus had been collected in the past.) Table 1 lists

these population samples, their sample sizes, field station numbers (KCE series), and museum catalog numbers. Maps giving the locations of field stations appear in Emberton (1994c). For reasons given above, population samples generally consisted of only one or a few live specimens, with a few exceptions from which up to 31 tissue samples were taken.

Tissue sampling and processing and starch gel electrophoresis followed methods detailed in Emberton (1988, 1994e). Loci used were *Aat-1*, *Aat-2*, *Est-1*, *Est-2*, *G6pd*, *Gpi*, *Lap*, *Mdh*, *Mpi*, *Pep-1*, *Pep-2*, and *6Pgd*. Thirty lanes were run per gel, with controls in lanes 1, 2, 8, 15, 16, 23, 29, and 30. The population of *Helicophanta souverbiana* Fischer, 1860, from station KCE164 was used as control, running each of its 30 samples on three or four separate gels. Questionable alleles were tested in adjacent lanes of the same gel, staggering samples when zymograms were particularly close. Polaroid photographs of all gels were used for final scorings.

Claustic analysis was performed using Hennig86 (Farris, 1988). Because of limitations in the Hennig86 program, the large number of alleles in some loci prevented using the locus as character, so alleles were used as independent characters (Mickevich & Mitter, 1981, 1983; Butth, 1984; Hillis & Moritz, 1990; Emberton, 1994d). *Clavator* was used as the outgroup, based on the limited anatomical evidence (Emberton, 1990) and the fact that this is the only Madagascan acavid genus known—as Cretaceous fossils only—on the African mainland (Jodot, 1939).

A representative shell of each species was mapped onto the resulting allozyme-based cladogram. At all polytomies, clades were arranged to minimize the degree of inferred evolutionary change in shell morphology. Shell evolution was qualitatively evaluated in the context of geographic ranges (as summarized in Emberton, 1990) and ecological niches (Emberton, 1994a; unpublished data).

RESULTS

Electrophoretic raw data are electromagnetically archived at *The Veliger* and at the Academy of Natural Sciences of Philadelphia (ANSP). In total, 105 alleles were detected. In addition, the MDH locus exhibited heteropolymers in all electrophoresed *Helicophanta*. The data yielded 71 informative characters (alleles plus heteropolymers); their distributions among populations are given in Table 2.

Claustic analysis produced 1718+ equally and maximally parsimonious trees with length 196, consistency index 0.36, and retention index 0.78. The resulting Nelson consensus tree showed considerable resolution, however, and is shown in Figure 1.

Allozymes uncovered no sibling species or cryptic species among the electrophoresed populations (Figure 1).

Figure 2 uses this phylogenetic hypothesis to parsimoniously track shell evolution among the 18 nominal species. Immediately obvious in Figure 2 is the polyphyly of *Heli-*

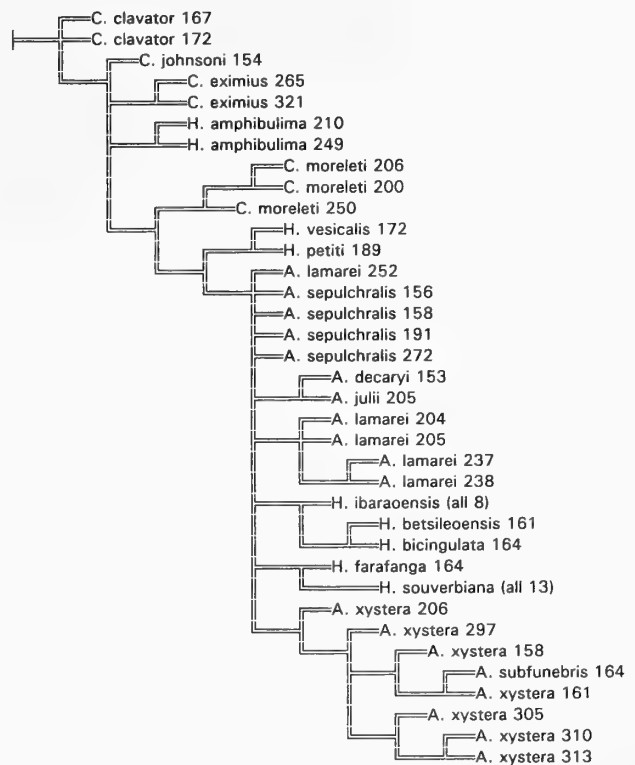


Figure 1

Nelson consensus tree of maximum-parsimony cladograms calculated from data in Table 2 by Hennig86. C. = *Clavator*, H. = *Helicophanta*, A. = *Ampelita*. Numbers refer to station numbers in the KCE series as listed in Table 1.

cophanta, with *H. amphibulima* Férussac, 1851, falling within *Clavator*. *Clavator*—even if expanded to include *H. amphibulima*—appears paraphyletic.

The remaining *Helicophanta* also appear paraphyletic and could even be polyphyletic. Comparing Figure 2 with species range maps (Emberton, 1990) and ecologies (Emberton, 1994a; unpublished data), it is clear that these *Helicophanta* underwent three separate regional radiations in both shell and ecological niche. The most conservative of these radiations comprises an eastern highland clade (*H. betsileoensis* Angas, 1879; *H. bicingulata* Smith, 1882; *H. ibaraoensis* Angas, 1879), all with similar, large, subglobose, dark brown shells, and all living on the rainforest floor. An eastern lowland clade consists of two rainforest species with disjunct shell shapes and ecologies: the tall-spined, ground-dwelling *H. farafanga*, and the subglobose, arboreal *H. souverbiana*; the shells of these two species share, however, a light background color interrupted by broad, spiral, reddish brown color bands. There is some geographic overlap between these two eastern clades, with, for example, *H. ibaraoensis* and *H. souverbiana* sympatric at mid-levels in Ranomafana National Park (east of Fiana-

Table 2

Presence/absence of informative allozyme characters (all autapomorphies deleted) among populations of Madagascan acavid land snails listed in Table 1. Characters are **1–5** *Aat-1* 105, 103, 102, 100, 97; **6–9** *Aat-2* 100, 99, 97, 95; **10–17** *Est-1* 114, 112, 108, 103, 102, 100, 94, 81; **18–25** *Est-2* 105, 103, 102, 100, 99, 97, 93, 91; **26** *G6pd* 100; **27–35** *Gpi* 115, 110, 107, 105, 103, 100, 99, 97, 91; **36–40** *Lap* 104, 102, 101, 100, 96; **41–49** *Mdh* hybrid heteropolymers, 100, 97, 96, 94, 92, 90, 89, 88; **50–56** *Mpi* 113, 110, 106, 105, 104, 100, 99; **57–62** *Pep-G* 100, 99, 98, 97, 93, 91; **63–67** *Pep-T* 104, 102, 100, 95, 94; **68–71** *6Pgd* 100, 98, 95, 93.

Species & local.	Character number														
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-71	
Adecar153	10000	10000	00000	00100	00000	10000	10000	01000	00010	00000	01000	01000	00001	00001	0
Ajuli1205	00001	01000	00000	00100	00000	10000	00100	00000	00010	00000	00000	01000	00001	00100	0
Alamar204	00001	01000	00010	00000	10100	10000	00010	01000	00010	00000	00100	00100	00000	10000	1
Alamar205	00001	01000	00111	00000	10100	10000	00010	01000	00010	00000	00100	00100	00000	10000	1
Alamar237	00001	01000	00100	00000	10000	10000	00010	01000	00010	00000	00100	00000	00000	10000	1
Alamar238	00001	01000	00100	00000	10000	10000	00010	01000	00010	00000	00100	00100	00000	10000	1
Alamar252	00001	01000	00110	00000	10000	10000	00100	01000	00010	00000	00100	00100	00001	00000	1
Asepul156	00010	00010	00000	000??	?????	10000	00010	01000	00010	00000	00100	00100	00001	00000	0
Asepul158	00001	01000	01000	00000	10000	10000	00001	01000	00010	00000	00100	00100	00001	00000	1
Asepul191	00001	01000	00010	00000	10100	10000	00011	01000	00010	00000	00100	00100	00001	00000	1
Asepul272	00001	01000	00010	00000	10000	10000	00001	01000	00010	00000	00100	00100	00001	00001	0
Asubful64	00001	00010	11000	00010	10000	10000	00011	11000	00010	00000	01000	01000	00001	00001	0
Axystr158	00001	01000	01000	00010	10000	10000	00010	01000	00010	00000	01000	01000	00010	00001	0
Axystr161	00001	00010	01000	00010	10000	10000	00010	01000	00010	00000	01000	01000	00010	00001	0
Axystr206	00001	01000	00000	00000	10000	10000	00010	10000	00010	00000	01000	00100	00010	00001	0
Axystr297	00001	01000	01000	00000	10000	10000	00010	10100	00010	00000	01000	01000	00010	00001	0
Axystr305	00001	01010	10000	00010	10000	10000	00100	10100	00010	00000	01000	01000	00010	00001	0
Axystr310	00001	01000	01000	00010	10000	10000	00100	00100	00010	00000	01000	01000	00010	00001	0
Axystr313	00001	01000	01000	00010	10000	10000	00100	00100	00010	00000	01000	01000	00010	00001	0
Cclava167	00010	00100	00000	10001	00000	00100	00000	00000	00000	01000	10000	00010	00100	00100	0
Cclava172	00010	00000	00000	10001	00000	00100	00000	00010	00000	01000	10000	00000	10100	00100	0
Cexims265	10000	00100	00001	00001	00000	00100	00000	00001	00000	01001	00000	00000	10100	00010	0
Cexims321	10000	00100	00001	00001	00000	00010	00000	00001	00000	01001	00000	00000	10100	00010	0
Cjohns154	01000	00100	00000	10001	00000	00010	00000	00010	00000	00000	10000	00000	01100	00010	0
Cmorel200	00100	10000	00000	01001	00001	01000	00000	10000	00000	10000	10000	00010	00100	00001	0
Cmorel206	00100	10000	00000	01000	00001	01000	00000	10000	00000	10000	10000	00010	00100	00001	0
Cmorel250	00000	10000	00000	00000	10000	01000	00000	10000	00000	10000	00000	00010	00100	00001	0
Hamphi210	00011	10000	00000	10000	00010	00000	00001	00010	00000	00010	00010	00000	01000	01010	0
Hamphi249	00001	10100	00000	10000	00010	00000	00001	00010	00000	00010	00010	00000	01000	01010	0
Hbetsi161	00001	01000	01010	00010	00000	10000	10000	10010	10100	00000	00000	10101	00001	00001	0
Hbicin164	00001	01000	01001	00010	01000	10000	10010	10010	10100	00000	00000	10101	00001	00001	0
Hfaraf164	00010	01000	01000	00000	00000	10010	00000	00010	10010	00000	00000	11000	00001	00010	0
Hibaro255	00001	01000	01000	00000	01000	10000	10000	00010	10000	00100	00010	00100	00001	00001	0
Hibaro262	00001	01000	00010	00000	01000	10000	00010	00010	10000	00100	00010	00100	00001	00001	0
Hibaro265	00001	01000	01000	00000	01000	10000	10010	00010	10000	00100	00010	00100	00001	00001	0
Hibaro270	00001	01000	00010	00000	01000	10000	01000	00010	10000	00100	00010	00100	00001	00001	0
Hibaro271	00001	01000	00010	00000	01000	10000	11000	00010	10000	00100	00010	00100	00001	00001	0
Hibaro273	00001	01000	00010	00000	01000	10000	10000	00010	10000	00100	00010	00100	00001	00001	0
Hibaro274	00001	01000	01000	00000	01000	10000	11010	00010	10000	00100	00010	01000	00001	00001	0
Hibaro279	00001	01000	01000	00000	01000	10000	00010	00010	10000	00000	00010	00100	00001	00001	0
Hpeti189	01000	00000	01000	00010	00000	10001	00000	10000	10001	00000	00010	00000	00000	00000	0
Hsouvr158	00010	10000	01001	00010	00000	10000	01000	01010	11000	00000	00001	01000	00001	00100	0
Hsouvr159	00010	10000	01000	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr161	00010	10000	01001	00010	10000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr164	00010	10000	00011	00010	10000	10000	01000	01000	11000	00000	00001	01000	00001	00100	0
Hsouvr296	00010	10000	00001	00010	00000	10000	01000	01010	11000	00000	00001	00000	00001	00100	0
Hsouvr297	00010	10000	00001	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr300	00010	10001	01001	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr302	00010	10000	00001	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr304	00010	10001	01001	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr305	00010	10000	00001	00010	00000	10001	00000	00010	11000	00000	00001	01000	00001	00100	0
Hsouvr308	00010	10001	01000	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100	0

Table 2

Continued.

Species & local.	Character number													
	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	56-60	61-65	66-71
Hsouv318	00010	10001	01000	00010	00000	10000	01000	00010	11000	00000	00001	01000	00001	00100 0
Hsouv322	00010	10000	01000	00010	00000	10001	00000	00010	11000	00000	00001	01000	00001	00100 0
Hvesic172	00010	10000	00010	00000	00000	10000	10010	01000	10001	00000	00000	00001	00000	00100 0

rantsoa: Emberton & Arijaona, in press), and *H. bicingulata* sympatric with both *H. farafanga* and *H. souverbiana* at low-level Manombo Reserve (south of Farafangana).

Well isolated from both of these, however, is a western clade comprising two species (*H. vesicalis* Lamarck, 1822; *H. petiti* Fischer-Piette, 1950) that differ from each other in shell size and shape but apparently not in ecology. Both species are semi-arid-land ground-dwellers that burrow into sand at the base of baobab trees and spiny bushes,

and both have light brown shells, but the shell of *H. petiti* is small for the genus and globose, whereas that of *H. vesicalis* is large and subglobose.

Ampelita could be polyphyletic within *Helicophanta* (Figure 2). The six nominal species of *Ampelita* fell into three distinct, two-species clades that are all geographically wide-ranging but that can be diagnosed conchologically. One of these clades contradicts current subgeneric taxonomy (Emberton, 1990) by grouping *Ampelita* (*Ampelita*)

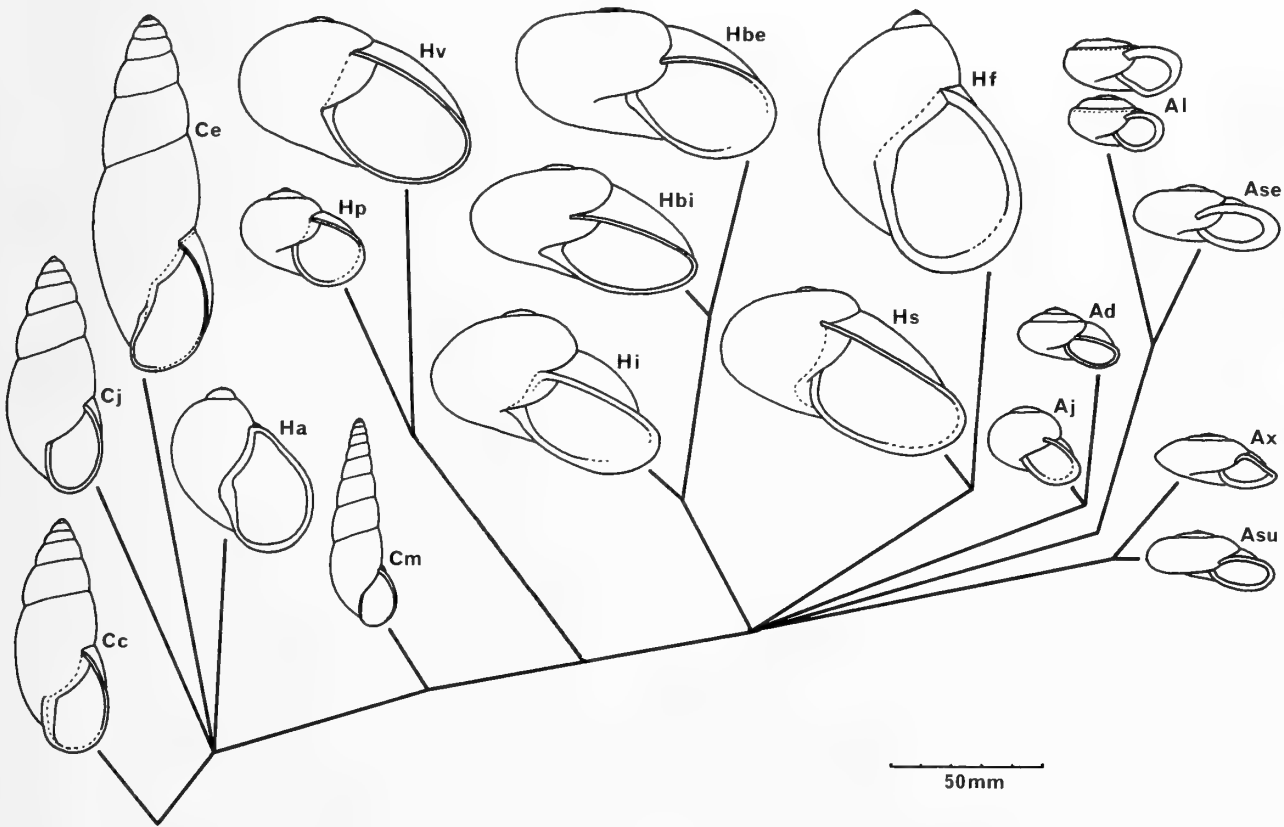


Figure 2

Shell evolution of the 18 nominal species of Madagascan acavids, based on the phylogenetic hypothesis of Figure 1. Ad = *Ampelita decaryi*, Aj = *A. julii*, Al = *A. lamarei*, Ase = *A. sepulchralis*, Asu = *A. subfunebris*, Ax = *A. xystera*, Cc = *Clavator clavator* Petit de la Saussaye, 1844, Ce = *C. eximius*, Cj = *C. johnsoni*, Cm = *C. moreleti* Férussac, 1851, Ha = *Helicophanta amphibulima*, Hbe = *H. betsileoensis*, Hbi = *H. bicingulata*, Hf = *H. farafanga*, Hi = *H. ibaraoensis*, Hp = *H. petiti*, Hs = *H. souverbiana*, Hv = *H. vesicalis*.

decaryi Fischer-Piette, 1952, and *A. (Eurystyla) julii* Fischer-Piette & Garreau de Loubresse, 1965. These two species have conchological similarities in their domed spires and sutural color bands, but are ecologically and geographically disjunct. *A. decaryi*, known only from the central part of Madagascar, is apparently a ground-dwelling burrower, whereas *A. julii*, known only from the northeast, seems to be arboreal.

The pair *A. lamarei* Pfeiffer, 1853, and *A. sepulchralis* Férussac, 1822, share the shell characters of a broadly flared apertural lip (but see intrapopulational variation in *A. lamarei*: Figure 2) and a wide, suprapraperipheral, spiral shell groove (pronounced in *A. lamarei*, more subtle in *A. sepulchralis*). These two have been suspected to be conspecific on the basis of shell similarities (Emberton, 1990: fig. 6); allozyme data support this hypothesis (Figure 1). Both *A. lamarei* and *A. sepulchralis* are extremely widespread in the island's eastern rain forest and seem to be semi- to fully arboreal.

Almost certainly conspecific are the extremely wide-ranging *A. xyстера* Pfeiffer, 1841, and the apparently localized southeastern *A. subfunnebris* Mabille, 1885–1886, which nests within *A. xyстера* in the cladogram (Figure 1). This also conflicts with current taxonomy, which erroneously puts the two into different subgenera (*A. (Xyстера)* Emberton, 1990, and *A. (Ampelita)* Beck, 1837: Emberton, 1990). The glossy, polymorphic shells (including various patterns of yellow and chestnut brown) of these two nominal taxa are virtually identical except for the angulate to keeled periphery of *A. xyстера*. Intraspecific variation from rounded to keeled peripheries is well known in land shells (Goodfriend, 1986). Both forms seem to be semi-arboreal.

Thus, in contrast to most *Helicophanta*, *Ampelita* shell morphology tends to indicate phylogenetic affinity but not ecology, which can differ greatly between closely related, similarly shelled species.

DISCUSSION

This study indicates that the magnificent radiation of Madagascar's relict acavids contains more conchological and ecological convergence than previously suspected. Noteworthy among the shell convergences (Figure 2) are those between "*Helicophanta*" *amphibulima* and *H. farafanga*; between *H. petiti* and globose *Ampelita* such as *A. julii*; and between *A. sepulchralis* and *A. subfunnebris*. Among the ecological convergences, the most striking is arboreality in both *H. souverbiana* and *A. julii*; this convergence is not evident in the shells, which are, respectively, lower and higher spired than those of their "sister species" (= closest known relatives).

The geographic segregation among three clades of *Helicophanta* suggests that these giant snails are extremely slow dispersers. This genus in particular may thus yield important new insights into Madagascan biogeography, once a robust phylogenetic hypothesis can be constructed for all

species. It can be hoped that *Clavator*, *Leucotaenius*, and *Ampelita* will prove useful as well, although *Leucotaenius* has few species and *Ampelita* seems less promising for biogeography based on the six taxa treated here. The prediction that worldwide acavoids will prove especially valuable for tracing ancient Gondwanan tectonic events (Emberton, 1990) is not falsified by these results.

The 99-species figure for Madagascan acavids is clearly inflated (Emberton, 1990). *Ampelita subfunnebris* should eventually be synonymized under *A. xyстера*, and other future synonymies probably should include *C. eximius* Shuttleworth, 1852, under *Clavator johnsoni* Smith, 1822, and *A. lamarei* under *A. sepulchralis*. If the 18 nominal taxa herein are considered a random sample, then 17% of Madagascan acavids will need synonymization, leaving 82 or 83 species-level taxa.

Although Figures 1 and 2 are only working hypotheses of phylogeny for only about 15 of the ca. 82 species of Madagascan acavids, they reflect the richest database yet available, and they contribute valuable insights into the evolution of this group (Emberton, 1994a). Anatomical data and more taxa will be added later; preliminary dissections of the terminal genitalia indicate that many characters are available in that system alone, predicting a robust hypothesis of their phylogeny. Taxonomic changes are postponed until then.

ACKNOWLEDGMENTS

Supported by grants from the National Science Foundation (DEB-9201060) and the American Philosophical Society to the author and by a grant from the National Institutes of Health (TMPAI1373) to Dr. George Davis. This paper is a contribution of the Molecular Genetics Laboratory of the Department of Malacology, Academy of Natural Sciences. Dr. Patricia Wright, International Director of the Ranomafana National Park Project, arranged for collecting and export permits for which I also thank the Malagasy government; Owen Griffiths assisted with transportation; Griffiths, Aldus Andriamamonjy, and many Malagasy villagers helped collect; Lu Xhang prepared, ran, and stained the electrophoretic gels; and Drs. David Lindberg and Barry Roth made useful comments on a previous draft.

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A Zoogeographic Review of the Cypraeidae (Mollusca: Gastropoda) Occurring in the Eastern Pacific Ocean

by

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Abstract. A zoogeographic review of the 24 species of Cypraeidae living in the eastern Pacific Ocean reveals the presence of 15 Indo-Pacific species, eight Panamic species, and one Californian species. The records of two additional taxa are discussed and rejected. The occurrences of these 24 cypraeid species are delineated for the eastern Pacific oceanic islands and the west American coastal regions. The available data suggest the presence in the eastern Pacific of mostly unstable cypraeid populations from the Indo-Pacific, whereas the species representing the Panamic and Californian faunal elements are composed of essentially stable populations, both in time and space.

Indo-Pacific immigrant species are contrasted with the long-established west American native element in terms of distribution and systematic composition. The Indo-Pacific *Erosaria caputserpentis* (Linnaeus, 1758), is used as an example to discuss the potential role of El Niño events on the dispersal of larvae from well-established central Pacific populations to the eastern Pacific Ocean.

INTRODUCTION

Biogeographic surveys of the marine biota of the eastern Pacific have shown that many families of marine mollusks have a component of species which has originated from other geographic regions (Carpenter, 1857; Keen, 1971). This component is small compared to the number of species thought to have arisen locally in west American tropics. It can be divided between species with Atlantic ancestry, the end result of the isolation caused by the closure of the Central American seaway, and species which have emigrated from the tropical Indo-Pacific.

The eastern Pacific has been referred to as a "recipient" region for species immigration, with the Indo-Pacific as the corresponding "donor" region, and there appears to be no documentary evidence of reverse immigration between these two areas (Vermeij & Rosenberg, 1993). It

can also be shown that the success of species which emigrate from the Indo-Pacific, measured as the ability of their propagules to establish a self-propagating population, is infrequent and dependent on a host of complex environmental factors, many of which are not yet understood (Vermeij, 1978; Kay, 1991).

The Cypraeidae in the eastern Pacific offer no exception to the generalized statements above. This family of gastropods is composed of both "resident" (endemic) and "immigrant" species, which are distributed in varying degrees along the continental margin and on the oceanic islands of the eastern Pacific. The Cypraeidae are accessible as a predominantly shallow-water group, and have a historic preeminence as the most popular group among shell collectors. Cypraeids are therefore likely to be gathered and recorded in collections, and thus are an ideal group for a survey of distribution and dispersal. This zoogeographic

review of all the Recent Cypraeidae occurring in the eastern Pacific Ocean contrasts emigrating Indo-Pacific species with their long established west American counterparts, and can be used to consider their abilities at dispersal.

In order to show apparent relationships among species groups, we have used available genus-group names to allocate the species rather than the traditional use of the genus *Cypraea sensu lato*. For zoogeographic analysis, this taxonomic usage seems preferable despite differences of opinion regarding the present classification of Cypraeidae (Kay, 1960a; Burgess, 1985).

MATERIALS AND METHODS

This study is based on a detailed review of faunal lists from published expedition reports, recent collection records, and the examination of specimens from the collections listed below. The present work complements data previously published by the senior author (Emerson, 1967, 1978, 1980, 1983, 1991, 1993). The Recent and fossil occurrences of cowries in the eastern Pacific were categorized according to their perceived geographic origin (immigrant versus endemic) and their distribution among the oceanic islands and west American mainland.

The validity of unique records of immigrant species (that is, a single report of a single specimen from a single locality) was judged using two criteria: the probability of a taxo-

nomic misidentification or the likelihood of the record being an artifact of human introduction.

The collection records from the following institutions were consulted for this study. Curators of all of these institutions were asked about their holdings for the oceanic islands, but some had no records for the Cypraeidae. The abbreviations listed accompany cited specimens in the text and figures: AMNH, American Museum of Natural History, New York; ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences, San Francisco; FMNH, Florida Museum of Natural History, Gainesville; LACM, Los Angeles County Museum of Natural History, California; UCMP, Museum of Paleontology, University of California, Berkeley; NMW, National Museum of Wales, Cardiff; SBMNH, Santa Barbara Museum of Natural History, California; SDNHM, San Diego Natural History Museum, California; USNM, National Museum of Natural History (U.S. National Museum collection), Smithsonian Institution, Washington, D.C.

RESULTS

A total of 24 cypraeid species were found to occur in the eastern Pacific on the oceanic islands and along the west American mainland. By far the largest faunal element is the Indo-Pacific constituent with 15 species (62%), followed by the Panamic element with eight species (33%),

Richard (Joe) Stephen Houbrick (1937–1993)

We dedicate this paper to the cherished memory of Dr. Houbrick, a longtime friend and valued colleague. "Joe" as he was known from his theological days, served on the curatorial staff in the Division of Mollusks of the U.S. National Museum of Natural History, from 1977 until his untimely death on August 27, 1993. For more than a year Joe had courageously battled the devastation of leukemia. Ironically, the cancer was in remission, when he suddenly succumbed to a fatal infection resulting in heart failure. His profound zest for life was an inspiration to all who knew him.

Joe will be fondly remembered for his keen sense of humor. A highly productive scientist, Joe leaves a prodigious legacy of scholarly contributions to the field of malacology. We extend our deepest sympathy to his family.

Joe Houbrick (far right) shown with (left to right) Jim McLean, Henry Chaney, and Bill Emerson at the Santa Barbara Museum of Natural History, California, in July, 1991 (photograph courtesy of J. H. McLean).



Table 1

Recent species of Cypraeidae known from the eastern Pacific oceanic islands and western American mainland.

	Clipperton Island	Revilla- gigedo Islands	Cocos Island	Galapagos Islands	West American mainland
A. Indo-Pacific species					
1. <i>Blasicrura alisonae</i> (Burgess, 1983) ^{18,19}	X ⁵	—	X ^{5,8,15}	X ¹	X ¹⁴
2. <i>Blasicrura teres</i> (Gmelin, 1791) ^{16,17,18}	X ⁵	—	—	X ^{1,5,6(?)}	X ^{3,5,13(?)}
3. <i>Erronea caurica</i> (Linnaeus, 1758)	—	—	—	—	X ^{2,5}
4. <i>Erosaria caputserpentis</i> (Linnaeus, 1758) ^{16,17,18}	X ²	—	X ^{8,15}	X ⁶	X ^{3,5,10,14}
5. <i>Erosaria helvola</i> (Linnaeus, 1758) ^{16,17,18}	X ²	—	—	—	—
6. <i>Lyncina lynx</i> (Linnaeus, 1758) ^{16,17,18}	—	—	—	—	X ²⁰
7. <i>Lyncina schilderorum</i> (Iredale, 1939) ^{16,17,18} = <i>L. arenosa</i> (Gray, 1824, not Dillwyn, 1823)	X ²	—	—	—	—
8. <i>Lyncina vitellus</i> (Linnaeus, 1758) ^{16,17,18}	X ^{2,5}	—	—	—	—
9. <i>Mauritia depressa</i> (Gray, 1824) ^{16,17,18}	X ²	—	—	—	—
10. <i>Mauritia maculifera</i> Schilder, 1932 ^{16,17,18}	X ^{2,5}	—	—	—	—
11. <i>Mauritia scurra</i> (Gmelin, 1791) ^{16,17,18}	X ²	—	—	—	—
12. <i>Monetaria annulus</i> (Linnaeus, 1758) ¹⁷	—	—	—	X ⁶	—
13. <i>Monetaria moneta</i> (Linnaeus, 1758) ^{16,17,18}	X ²	—	X ^{2,8,15}	X ^{2,6,21}	X ²¹
14. <i>Staphylaea staphylaea</i> (Linnaeus, 1758) ¹⁶	—	—	—	—	X ^{2,5}
15. <i>Talparia talpa</i> (Linnaeus, 1758) ^{16,17,18}	—	—	X ^{8,12,15}	—	X ⁴
B. Panamic species					
1. <i>Erosaria albuginosa</i> (Gray, 1825)	X ²	X ^{9,12}	X ^{2,7,11,15}	X ²	X ²
2. <i>Luria isabellamexicana</i> (Stearns, 1893)	X ²	X ^{9,12}	X ^{11,15}	X ^{2,7}	X ²
3. <i>Macrocypaea cervinetta</i> (Kiener, 1843)	—	—	X ^{5,15}	X ⁷	X ²
4. <i>Zonaria aequinoctialis</i> Schilder, 1933	—	—	—	—	X ²
5. <i>Zonaria annettae</i> (Dall, 1909)	—	—	—	—	X ²
6. <i>Zonaria arabicula</i> (Lamarck, 1811)	—	X ¹²	—	X ^{1,7}	X ²
7. <i>Zonaria nigropunctata</i> (Gray, 1828)	—	—	—	X ⁶	X ²
8. <i>Zonaria robertsi</i> (Hidalgo, 1906)	—	—	X ^{5,15}	X ⁶	X ²
C. Californian species					
1. <i>Zonaria spadicea</i> (Swainson, 1823)	—	—	—	—	X ²
D. Rejected records					
1. Indo-Pacific					
<i>Blasicrura rashleighana</i> (Melvill, 1888) ¹⁸	X ²	—	X ⁵	—	—
2. Western Atlantic					
<i>Erosaria spurca acicularis</i> (Gmelin, 1791)	—	—	X ⁵	—	—

1 = Burgess, 1985; 2 = Cate, 1969; 3 = Cantera, 1986, 1991; 4 = Emerson, 1983; 5 = Groves, 1992; 6 = Kay, 1991; 7 = Keen, 1971; 8 = Shasky, 1983, 1985, 1989a, b; 9 = Strong & Hanna, 1930; 10 = Tomlin, 1927; 11 = AMNH coll.; 12 = LACM coll.; 13 = Birkeland et al., 1975; 14 = recorded herein; 15 = Groves, 1993a; 16 = reported from French Polynesia (Richard, 1985); 17 = reported from the Line Islands (Kay & Switzer, 1974); 18 = reported from the Hawaiian Islands (Kay & Schoenberg-Dole, 1991); 19 = reported from the Marquesas and Society Islands (Burgess, 1985); 20 = Chaney, 1993; 21 = Emerson, 1993.

and Californian with one (5%); see Table 1. The report of a single western Atlantic species is questioned in the following discussion. Of these 24 taxa, only representatives of the Panamic and Californian faunal species are known from the fossil record (Plio-Pleistocene) of the western Americas (Table 2).

All eight species of the Panamic cypraeids occur along the west American mainland; six of these (75%) are recorded in the Galapagos Islands; four (50%) on Cocos Island; three (38%) in the Revillagigedo Islands; and two (25%) on Clipperton Island (Table 1).

In contrast, eight of the 15 Indo-Pacific species (53%) are known only from the oceanic islands. Of these 15 taxa,

Clipperton Island has 10 species (66%), the Galapagos Islands have five species (33%), and Cocos Island has four species (26%). Eight of the 15 Indo-Pacific species are known from the mainland (53%). No Indo-Pacific cypraeids are known from the Revillagigedo Islands (Table 1).

The Indo-Pacific species most widespread in the eastern Pacific was *Erosaria caputserpentis* (Linnaeus, 1758), which has been found from the west American mainland and all the oceanic islands, with the exception of the Revillagigedos. Records for *Erosaria caurica* (Linnaeus, 1758), *Lyncina lynx* (Linnaeus, 1758), *Staphylaea staphylaea* (Linnaeus, 1758) and *Erosaria spurca acicularis* (Gmelin, 1791)

Table 2

Fossil records of the Recent species of Cypraeidae known from the eastern Pacific oceanic islands and western American mainland. Records refer to Pleistocene deposits unless otherwise indicated: A = Plio-Pleistocene records.

	California	Baja California, Mexico [Pacific coastal region]	Gulf of California, Mexico	Tres Marias Is-lands, Mexico	Oaxaca, Mexico	Ecua-dor	Gala-pagos Is-lands
A. Indo-Pacific species							
1. <i>Blasicrura alisonae</i> (Burgess, 1983)	—	—	—	—	—	—	—
2. <i>Blasicrura teres</i> (Gmelin, 1791)	—	—	—	—	—	—	—
3. <i>Erronea caurica</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
4. <i>Erosaria caputserpentis</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
5. <i>Erosaria helvola</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
6. <i>Lyncina lynx</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
7. <i>Lyncina schilderorum</i> (Iredale, 1939) = <i>L. arenosa</i> (Gray, 1824, not Dillwyn, 1823)	—	—	—	—	—	—	—
8. <i>Lyncina vitellus</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
9. <i>Mauritia depressa</i> (Gray, 1824)	—	—	—	—	—	—	—
10. <i>Mauritia maculifera</i> Schilder, 1932	—	—	—	—	—	—	—
11. <i>Mauritia scurra</i> (Gmelin, 1791)	—	—	—	—	—	—	—
12. <i>Monetaria annulus</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
13. <i>Monetaria moneta</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
14. <i>Staphylaea staphylaea</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
15. <i>Talparia talpa</i> (Linnaeus, 1758)	—	—	—	—	—	—	—
B. Panamic species							
1. <i>Erosaria albuginosa</i> (Gray, 1825)	—	—	X ^{9,10,13A,16}	—	—	X ²⁰	—
2. <i>Luria isabellamexicana</i> (Stearns, 1893)	—	—	—	—	—	—	—
3. <i>Macrocypraea cervinetta</i> (Kiener, 1843)	—	—	—	—	—	—	X ^{4,13A}
4. <i>Zonaria aequinoctialis</i> Schilder, 1933	—	—	—	—	—	—	—
5. <i>Zonaria annettae</i> (Dall, 1909)	—	X ^{2,3,11,14,18}	X ^{5,6A,7,8,10A,12,14,16}	—	—	—	—
6. <i>Zonaria arabicula</i> (Lamarck, 1811)	—	X ^{2,8,9,10,11,18,19}	X ^{9,11}	X ^{9,15}	X ^{12,13,19}	—	—
7. <i>Zonaria nigropunctata</i> (Gray, 1828)	—	—	—	—	—	—	X ^{13,17}
8. <i>Zonaria robertsi</i> (Hidalgo, 1906)	—	—	—	—	—	—	—
C. Californian species							
1. <i>Zonaria spadicea</i> (Swainson, 1823)	X ^{1,12A,13A,14,21}	X ^{2,3,8,9,18}	—	—	—	—	—

1 = Arnold, 1903; 2 = Chace, 1956; 3 = Dall, 1918; 4 = Dall & Ochsner, 1928; 5 = Dowlen & Minch, 1973; 6 = Durham, 1950; 7 = Emerson, 1960; 8 = Emerson, 1980; 9 = Emerson & Old, 1963; 10 = Emerson & Hertlein, 1964; 11 = Emerson in Squires, 1959; 12 = Grant & Gale, 1931; 13 = Groves, 1993a; 14 = Groves, 1993b; 15 = Hertlein, 1934; 16 = Hertlein, 1957; 17 = Hertlein, 1972; 18 = Jordan, 1936; 19 = Palmer & Hertlein, 1936; 20 = Rivera, 1953; 21 = Woodring & Bramlette, 1946; 22 = Kellogg (1976) and Lindberg et al. (1980:53, fig. 2) reported specimens of the Indo-Pacific *Erosaria cernica* (Sowerby, 1870) from Pleistocene deposits on Guadalupe Island, Baja California, Mexico. This is the sole fossil record for a Recent cypræid Indo-Pacific faunal species known from the eastern Pacific region (Emerson, 1991:67). No fossiliferous deposits are known from Clipperton Island, the Revillagigedo Islands and Cocos Island.

are unique occurrences, not having been corroborated by the collection of additional specimens. Records attributable to *Blasicrura rashleighana* (Melville, 1888) are rejected due to the misidentification of these specimens.

DISCUSSION

In this study, a distinction is made between taxa which are "residents" along the west American mainland (New World species) and those which are "immigrants," having been derived from the Indo-Pacific. Reporting the distri-

bution of species through the eastern Pacific, based on their presence or absence from diverse localities, is essential data for understanding the biogeography of the Cypraeidae. Unfortunately, specific life history information for these taxa, such as reproductive cycles and the intensity of larval dispersal, is virtually unknown and must be inferred from the general knowledge of the Cypraeidae as a whole.

West American Species

Nine species (eight Panamic, one Californian) are recognized as residents of the eastern Pacific. All species occur

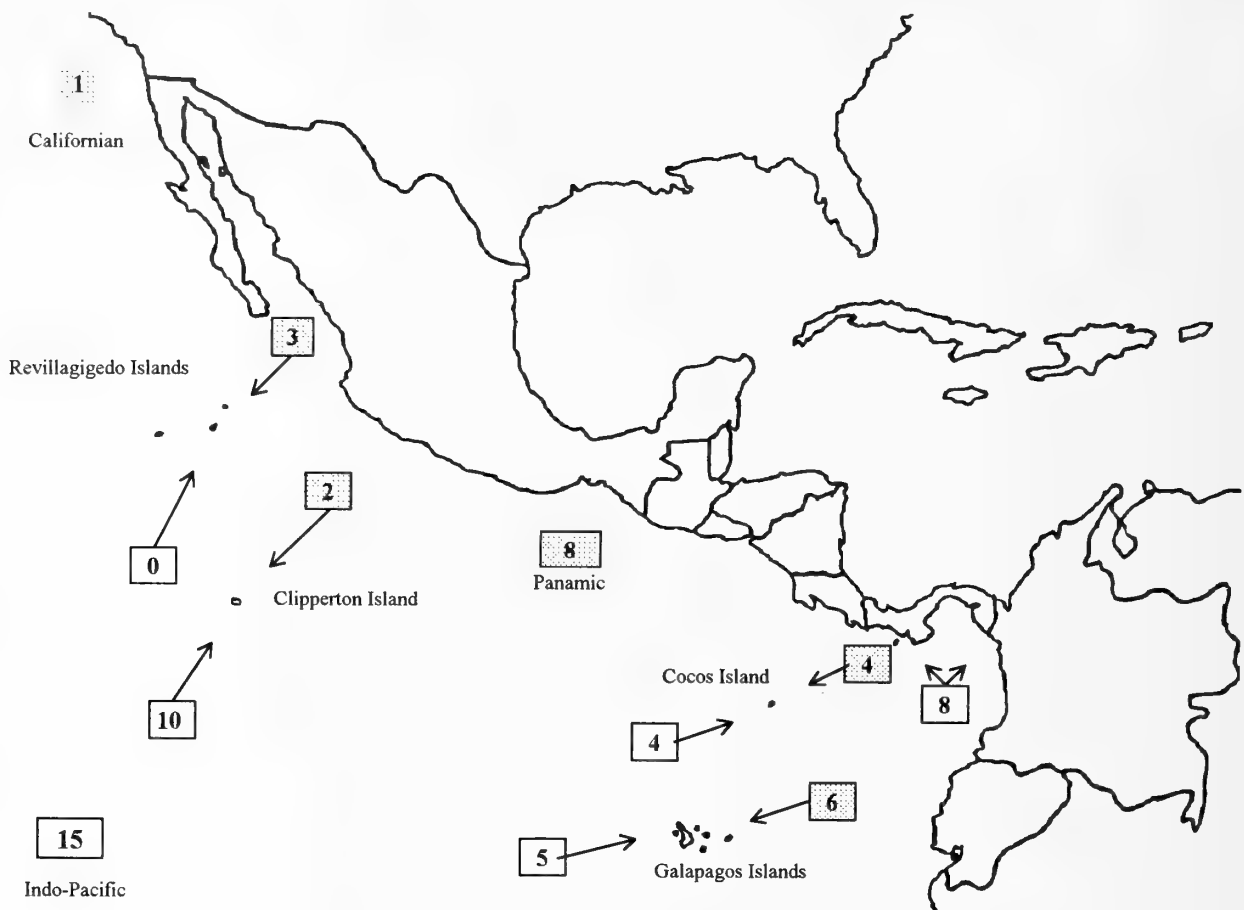


Figure 1

The origin and distribution of the eastern Pacific Cypraea. Occurrences of emigrating species from the Indo-Pacific (total number = 15) on oceanic islands and the west American mainland are denoted by white boxes. Records of Panamic species (total number = 8) on oceanic islands denoted by shaded boxes. All Panamic species occur on mainland. A single species is known from the Californian Province.

on the west American mainland, whereas some are absent on the oceanic islands (Figure 1). The eight Panamic species can further be divided between those taxa which appear to have derived from within this region and those which are closely related to living Indo-Pacific species.

Of the first group, six Panamic species are of New World derivation. Of these, *Macrocypraea cervinetta* (Kiener, 1843) is a cognate of the western Atlantic *M. cervus* (Linnaeus, 1758) and is reported from the Plio-Pleistocene of the Galapagos Islands and the Pleistocene of Ecuador (Table 2), while *Zonaria annettae* (Dall, 1909) (Gulf of California and Pacific Baja California [Burgess, 1985]) and *Z. aequinoctialis* Schilder, 1933 (Nicaragua to Peru) are closely related species that have widely disjunct ranges. Until recently, these two taxa were considered to represent a polytypic species (cf. Burgess, 1985; Keen, 1971). *Zonaria annettae* is known from several Baja Californian and west Mexican Plio-Pleistocene deposits (Table 2). *Zonaria em-*

makingae, recently recognized as a precursor of *Z. annettae*, was described by Groves (1994) from the lower to middle Miocene (Topanga Canyon Formation, Santa Monica Mountains) of Los Angeles County, California.

Zonaria nigropunctata (Gray, 1828) is limited in distribution to the Galapagos Islands, where it occurs in Plio-Pleistocene deposits (as *Z. darwini* [Ingram, 1948]) (Table 2), and the mainland from Ecuador and Peru. Of the eight west American cypraeids, only three, *Erosaria albuginosa* (Gray, 1825), *Zonaria robertsi* (Hidalgo, 1906), and *Z. arabicula* (Lamarck, 1810) have extensive distributions on the mainland (Gulf of California, Mexico to South America). *Erosaria albuginosa* (Plio-Pleistocene) and *Z. arabicula* (Pleistocene) are also reported from the fossil record of western America (Table 2).

Only two of the eight west American native taxa appear to be closely related to living Indo-Pacific species. The first of these, *Luria isabellamexicana* (Stearns, 1893) was con-

sidered by some authors (e.g., Ingram, 1951) to be a subspecies of *L. isabella* (Linnaeus, 1758), a wide-ranging Indo-Pacific species (Red Sea to Central Pacific Ocean). The two taxa, however, differ in anatomical and shell characters (Emerson & Old, 1963; Burgess, 1985). The presence of the *L. isabella-isabellamexicana* complex in the New World appears to date from the Neogene of the Caribbean region, as noted by Pilsbry (1922), Woodring, 1928), and Ingram (1951). These authors considered *Cypraea patrespatriae* Maury, 1917, described from the Gurbabo Formation, middle Miocene of the Dominican Republic, to be remarkably similar in shell characters to *L. isabella*. They also remarked on the close similarity of Maury's taxon to west Mexican specimens of *L. isabellamexicana*. The populations in Jamaica, Dominican Republic, Trinidad, and Venezuela (Ingram, 1951) apparently became extinct in the western Atlantic sometime during the Pliocene. *Luria isabellamexicana*, however, has not yet been reported from the Neogene record of the western Americas, but from Mexico to Guatemala fossiliferous deposits of this period are largely limited to exposures in the Tres Marias Islands and the Gulf of California region (Emerson, 1991). Foin (1976) considered *L. isabellamexicana* and *L. cinerea* (Gmelin, 1791) from the western Atlantic to be cognates. However, the shells and the mantles of these two species differ considerably (cf. Burgess, 1985), and *L. cinerea* is most likely a sister taxon of *L. lurida* (Linnaeus, 1758) from the eastern Atlantic (Lorenz & Hubert, 1993).

Erosaria albuginosa (Gray, 1825) is the second west American species with a living Indo-Pacific counterpart. It may be compared with *Erosaria poraria* (Linnaeus, 1758), a species distributed from east Africa to the central Pacific Ocean. Despite general similarities, these species can be differentiated on the basis of anatomical and shell characters (Burgess, 1985). A third species, *Erosaria engleri* (Summers & Burgess, 1965) also appears related to *E. albuginosa* and *E. poraria*. This taxon is restricted to Easter Island and Sala y Gomez Island.

Both *L. isabellamexicana* and *E. albuginosa* are common at Clipperton Island (Hertlein & Allison, 1960; Cate, 1969). The latter taxon is known from Plio-Pleistocene deposits in the Gulf of California (Table 2).

Zonaria spadicea (Swainson, 1823) ranges from Monterey, California, to Cedros Island, Baja California Sur, Mexico (McLean, 1978) and is the only cypraeid represented in the Californian faunal province. This species thrives in the temperate waters of southern California, where it dates back to the middle to late Pliocene, as *Cypraea fernandoensis* Arnold, 1907, from the Pico Formation near Newhall, Los Angeles County, California (Cate, 1969).

Indo-Pacific Species

The distribution of the 12 Indo-Pacific cypraeids found in the eastern Pacific is mostly restricted to the oceanic

islands in an attenuated pattern similar to other prosobranch gastropods with west Pacific affinities (Emerson, 1991). More cowrie species were reported from Clipperton Island than any other locality in the region (Cate, 1969; Groves, 1992). As shown in Table 1, the only records from the eastern Pacific of *Mauritia maculifera* (Schilder, 1932), *Mauritia depressa* (Gray, 1824), *Mauritia scurra* (Gmelin, 1791), *Lyncina vitellus* (Linnaeus, 1758), *Lyncina schilderorum* (Iredale, 1939), and *Erosaria helvola* (Linnaeus, 1758) are those from collecting surveys at Clipperton made in 1956 and 1958. With the exception of *M. depressa* and *E. helvola*, which were live taken intertidally, all these other taxa were collected as dead and eroded specimens from beach drift (Hertlein & Allison, 1960). So far the deeper waters around Clipperton, accessible by SCUBA, are still relatively undocumented (Emerson, 1993) and need to be sampled in a manner similar to the recent surveys at Cocos Island (Shasky, 1983, 1985, 1989c).

Other Indo-Pacific cowries include *Monetaria annulus* (Linnaeus, 1758), a very common western Pacific species reported from the eastern Pacific as a single specimen from the Galapagos Islands (Kay, 1991), and *Talparia talpa* (Linnaeus, 1758) which has been found intermittently during the past decade at Cocos Island and in the nearshore waters of western Panama (Emerson, 1993; Skoglund, 1992).

The remaining Indo-Pacific taxa listed in Table 1, *Blasicrura teres* (Gmelin, 1791), *Blasicrura alisonae* (Burgess, 1983), *Erosaria caputserpentis* (Linnaeus, 1758), and *Monetaria moneta* (Linnaeus, 1758) are the best represented in the eastern Pacific. References to the first two species have been taxonomically confused, whereas the biology of *E. caputserpentis* is the best known of this group and allows for several generalizations to be made about the dispersal capabilities of the immigrating cypraeids.

The *Blasicrura* "teres-alisonae" Species Group

Although specimens are widespread throughout the Indo-Pacific, the systematics of *Blasicrura teres* and its related species are in need of critical taxonomic review which considers both shell characters and anatomy. Burgess (1983) described *B. alisonae* from Hawaii, separating it from *B. teres* based on mantle characters. We are retaining the use of *B. alisonae* at present, despite the recent work of Lorenz & Hubert (1993, see below). Populations in French Polynesia (Society Islands and Marquesas) have been subsequently attributed to this new species (Burgess, 1985) as have specimens recently collected in the eastern Pacific at Cocos Island and along western Panama. Eastern Pacific faunal records made prior to Burgess' description of *E. alisonae* in 1983 from the eastern Pacific would obviously predate this distinction.

Therefore, while we have cited *B. teres* from Clipperton Island, the Galapagos Islands, and the west American mainland (Table 1), these records are questionable. In each case, determinations were based on dead-collected,

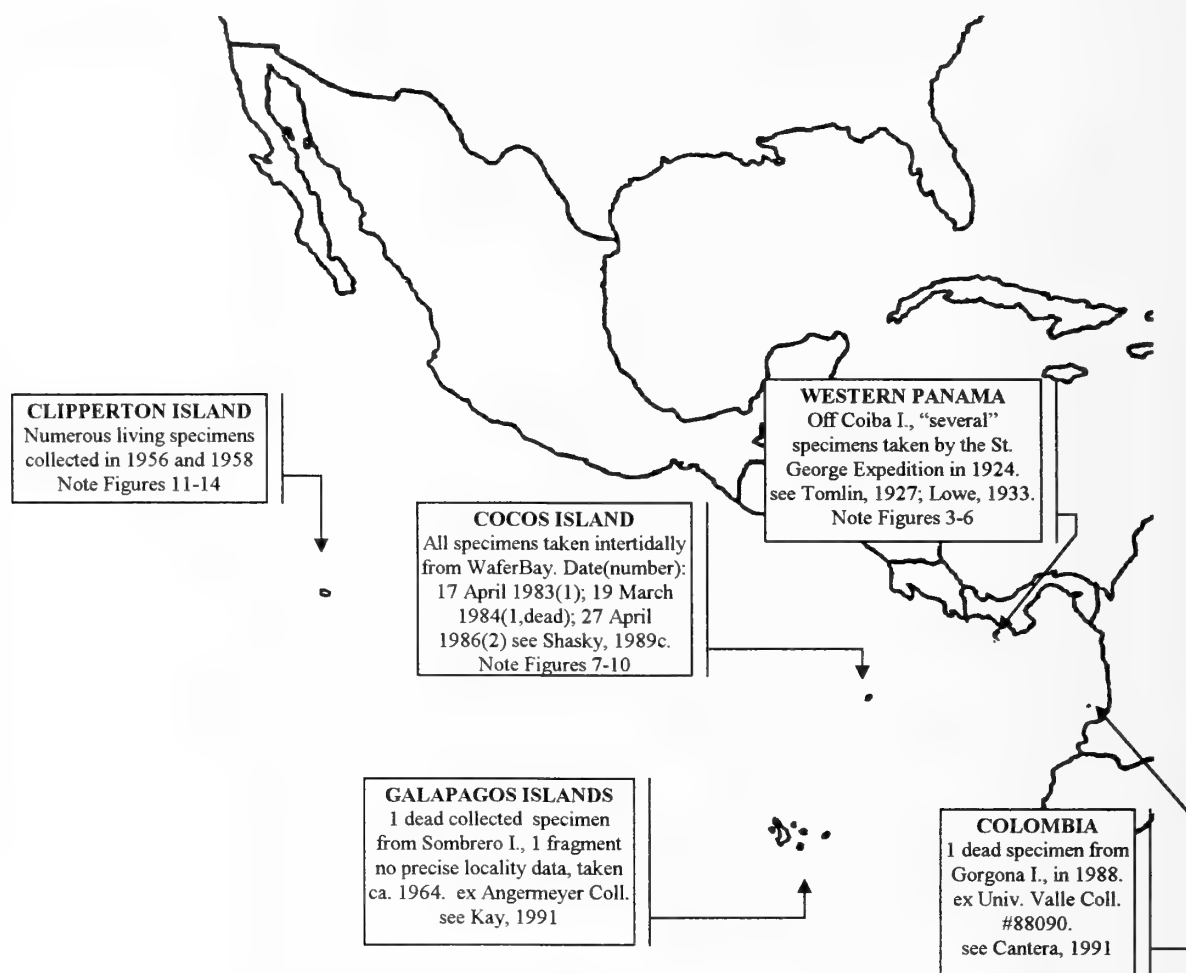


Figure 2

Records of the occurrence in the eastern Pacific of *Erosaria caputserpensis*, the most widespread Indo-Pacific cypraeid immigrant. Refer to Figures 3-14 for additional information on disposition of specimens.

often decorticated specimens and were initially reported prior to 1983.

Recent collections made by the junior author at Cocos Island (1991-1992) and on the Pacific coast of Panama (1993) have compiled a significant number of specimens of this group. All of these cowries had the mantle characters of *B. alisonae* and not of *B. teres*, even though there was considerable variation in shell morphology, expressed as differences in color pattern, growth form, or most importantly, sexual dimorphism. Populations from Cocos Island and western Panama have a similar radular morphology (*teste* Hugh Bradner, June 26, 1993).

Further elaboration on the characteristics of *B. alisonae* in the eastern Pacific is the subject of current work in progress by the junior author, based on these recent collections. It is noted, however, that Lorenz & Barbier (1992) initially consigned *B. alisonae* to the synonymy of *B. alveolus*

(Tapparone-Canefri, 1882) from the west Indian Ocean, which they considered to be a subspecies of *B. teres*. Subsequently, Lorenz & Hubert (1993) placed *B. alisonae* in synonymy with *B. teres pellucens* (Melvill, 1888) and treated the latter taxon as an "ecological subspecies" of *B. teres sensu stricto*. In reporting the geographic distribution of both of these taxa, which occur sympatrically throughout the entire tropical Indo-Pacific, they attributed all records of the "teres" group in the eastern Pacific to *B. teres pellucens*.

Erosaria caputserpensis

Erosaria caputserpensis is a common, distinctive, and widely distributed species typically found in the very shallow waters around coral reefs and rocky intertidal margins throughout the Indo-Pacific. In the eastern Pacific it has

been recorded from the oceanic islands and the west American continental margin. These locality records are illustrated in Figure 2.

Erosaria caputserpentis is comparable to *E. caputdraconis* (Melvill, 1888), an endemic species from Easter Island and Sala y Gomez Island in the southwest Pacific (Griffiths, 1958; Rehder, 1980; Tissot, 1982, 1988). The two species differ in that *E. caputdraconis* has a more concave base, coarser teeth with black interstices, and a finer pattern of white spots on the dorsum (Burgess, 1985; Lorenz & Hubert, 1993). *Erosaria caputserpentis* is not known from either of these islands (Burgess, 1985).

The functional morphology (Kay, 1960b) and the early life history (Ostergaard, 1950) of the Hawaiian populations of *E. caputserpentis* are well documented. Like other tropical cypraeids, it has an indirect larval development, in contrast to the direct mode of development in some temperate species (Anderson, 1965; Liltved, 1989). Some tropical cowries are reported to have high rates of fecundity, with from 10,000 to 500,000 veligers issued from a single egg mass (Wilson, 1985). After spending up to four weeks in the egg capsule, veligers are then released and in some cases can spend several weeks in the plankton before sinking to the bottom (Kay, in Burgess, 1985; Kay, 1990). In the case of Hawaiian specimens of *E. caputserpentis*, the size of an egg was determined to be ca. 90 μm , and the larvae were found to hatch after about 18 days in capsule at a size of 100–200 μm (Taylor, 1975).

Calculating the period in which the larvae of *E. caputserpentis* can successfully remain viable in the plankton is dependent on a host of biological and environmental assumptions. In Hawaii, Taylor (1975) found the pelagic larval stage of *Erosaria* species to exist in the plankton for a period of 10 days to 2 weeks, a time span too short for a transit to the eastern Pacific, (e.g., Line Islands to Clipperton), which Finet (1991) has calculated would take 4 to 5 months via the North Equatorial Counter Current. Because much of larval settlement behavior is dependent on being exposed to the correct environmental "cues," the actual time larvae may remain in the plankton and also remain viable could be extended if those cues are not present (Gosliner, 1987). Cypraeid larvae were recorded by Scheltema (1986) to constitute approximately 13% of the plankton from 27 of the 163 station samples containing gastropods analyzed by him in the central Pacific.

Attempts to determine the potential insular sources for the introduction of larvae into the eastern Pacific from the west (Line Islands, French Polynesia, Hawaiian Islands) by comparison of shell characters is probably not possible because the number of specimens available from the eastern Pacific localities is limited and the levels of intra-population variability of this species is great (Tissot, 1984). While Schilder & Schilder (1938) recognized six geographical races of *E. caputserpentis* in the Indo-Pacific largely on the basis of shell characters, most workers now do not accord subspecific status to the regional populations (Bur-

gess, 1985). However, Tissot (1984) demonstrated overall differences in specimens from the Hawaiian Islands, where this species dates from the Pleistocene (Ostergaard, 1928). He determined on the basis of a multivariate analysis that Hawaiian specimens are "... distinctly smaller and more marginated, and possess more numerous basal teeth than individuals from the Indo-Pacific." Hawaiian specimens were named *E. c. caputophidii* by Schilder (1927).

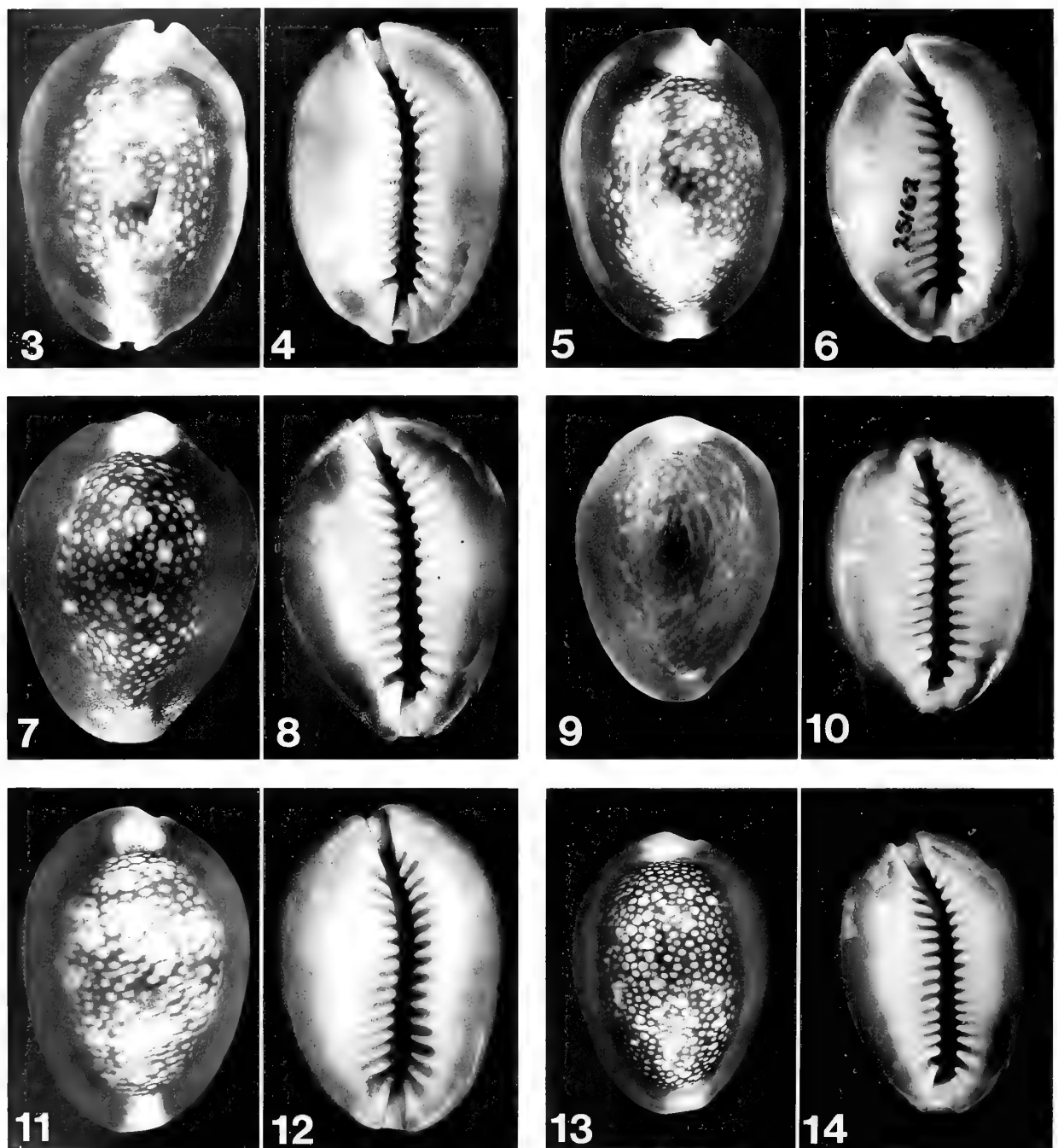
Lorenz & Hubert (1993) recognized *E. c. caputophidii* as a valid subspecies, differing from the nominate subspecies by having a darker base, brownish interstices between the teeth and an angular "hardly expanded" margin (somewhat at variance with Tissot's finding above). In addition they have extended the range of this subspecies to include the Marquesas Islands where specimens with brownish interstices also occur (e.g., Ua Huka, Marquesas Islands, AMNH 250142). However, these shell characters are not consistent throughout entire populations, as specimens with white interstices are also present in Hawaiian and the central Pacific populations (e.g., Nanakuli Reef, Oahu, Hawaii, AMNH 219601; Hiva Oa, Marquesas Islands, AMNH 250140).

Examination of eastern Pacific specimens shows the same range of variation as found in central Pacific populations (Figures 3–14). Specimens with brownish interstices are known from western Panama (Figures 5, 6), Cocos Island (Figures 9–10), and Clipperton Island (Figures 11–14), but other specimens from Panama (Figures 3, 4) and Cocos Island (Figures 7, 8) have white interstices, resembling the nominate subspecies. Although shell characters alone may not be useful in tracing the insular path of recruitment to the eastern Pacific, this species is common enough to provide enough material for a more detailed genetic study when resources permit.

Unique and Rejected Records

In addition to the taxa discussed above, four additional Indo-Pacific species and one Atlantic species have been reported in the eastern Pacific. These are: *Erronea caurica*, *Staphylaea staphylaea*, *Lyncina lynx*, *Blasicrura rashleighana*, and *Erosaria spurca acicularis*. Localities of each record and the date of discovery are shown in Figure 15.

Records for *E. caurica* and *S. staphylaea* are based on single beachworn specimens found by Helen DuShane in 1956 near Cape San Lucas. Each specimen was figured by Cate (1969) and was correctly identified, despite being beachworn. These are unique records of the occurrence of these species in the eastern Pacific and, based on their known distribution, we question whether they have naturally immigrated to the Baja peninsula or are artifacts of human introduction. Neither species is known to occur in the Hawaiian archipelago (Kay, 1979; Burgess, 1985; Lorenz & Hubert, 1993), and *E. caurica* is not known from French Polynesia (Burgess, 1985; Richard, 1985). *Staphylaea staphylaea* does occur in the Society Islands and



Explanation of Figures 3-14

Erosaria caputserpentis; $\times 1.5$. Figures 3-6, off Coiba Island, Panama (Figures 3-4, NMW 1955.158. 652; Figures 5, 6, SDNHM 25162). Figures 7-10, Wafer Bay, Cocos Island, D. R. Shasky collection (Figures 7, 8, 19 March 1984; Figures 9, 10, 17 April 1983). Figures 11-14, Clipperton Island (Figures 11, 12, AMNH 204598b; Figures 13, 14, AMNH 204598c). Both of the specimens from Clipperton Island (ventral aspects, Figures 12, 14), one of the specimens from Cocos Island (ventral aspect, Figure 10), and one of the specimens from Panama (ventral aspect, Figure 6) have some brownish interstices between the teeth. The other specimens have whitish interstices.

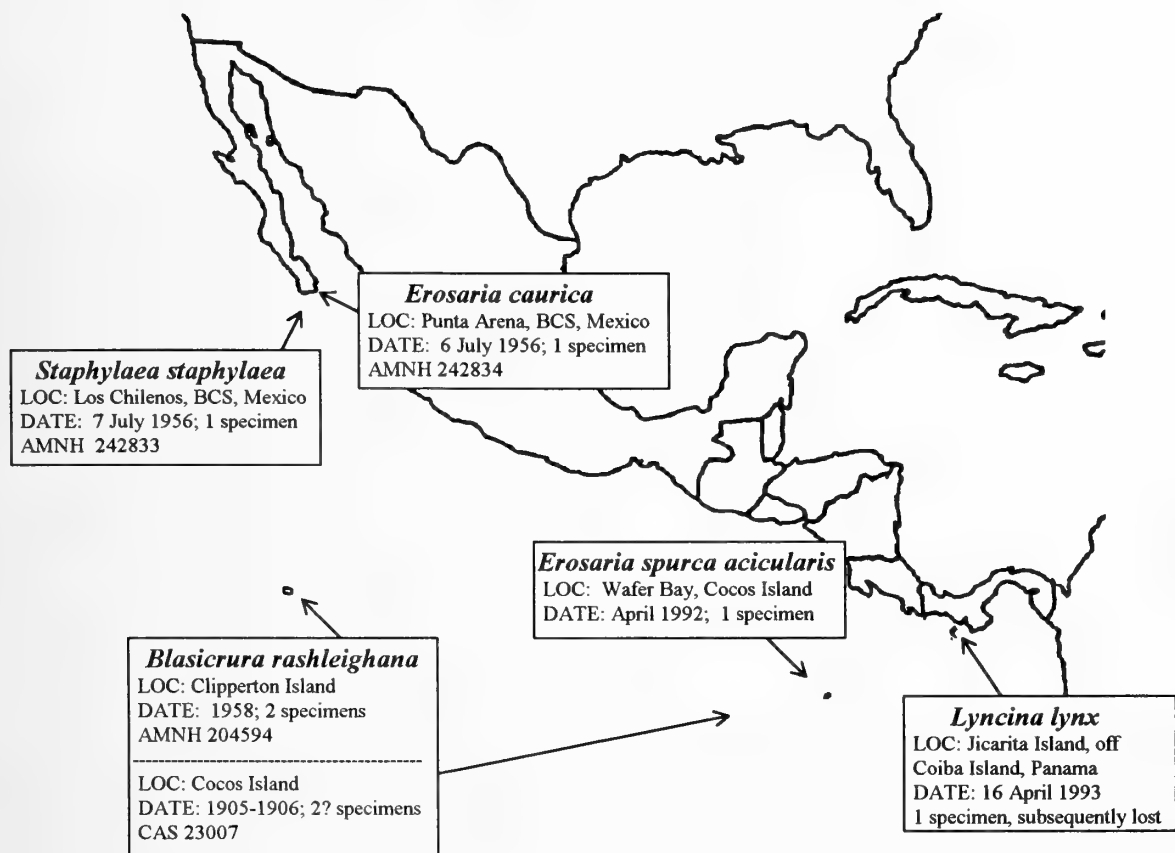


Figure 15

Species of cypraeids with unique records of occurrence in the eastern Pacific and those with records which are either questioned or rejected by this study. Refer to text for detailed discussion.

the Tuamotu Archipelago (Richard, 1985), and has been reported from Johnson Island (Burgess, 1985). Unlike most regions of Baja California, the coastline between Cape San Lucas and Cape Pulmo has been an active recreational area for over 50 years. No other Indo-Pacific cypraeid has yet been found either in Baja California or the offshore Revillagigedo Islands. Given that all corroborated records of Indo-Pacific cypraeids reported from the west American mainland are from the southern Panamic region, our acceptance of these records as evidence of a natural distribution is provisional.

A third unique record is the recent report of a single, dead adult *Lyncina lynx* being found from the Gulf of Chiriqui, Panama (Chaney, 1993). The specimen was subsequently lost by its collector after its identification was verified. Several factors suggest that this record is the result of a natural occurrence. First, the specimen was discovered *in situ* in a coral rubble habitat consistent with its known environment in the tropical Indo-Pacific. Second, the collection locality was well removed from any potential anchorages, which would greatly lessen the chances of it being

passively discarded from a vessel (it could not have just been dropped overboard). Third, *L. lynx* is as widespread in the Indo-Pacific as are other cypraeids now reported from the eastern Pacific (e.g., *E. caputserpentis*, *M. moneta*, *B. alisonae*, and *T. talpa*) and, fourth, western Panama is the most likely mainland site for the settlement of an Indo-Pacific immigrant as evidenced by records of all four of the above taxa being collected from the same region. We accept this new record with reservation, awaiting additional evidence.

Blasiverrura rashleighana was reported by Ingram (1945) in the eastern Pacific from a single specimen obtained on Cocos Island by the 1905-1906 Expedition of the California Academy of Sciences. This specimen is apparently lost as the measurements of the specimen cited by Ingram (1951), "25 mm, 17 mm broad" do not match those for the specimen (33 mm long × 20.5 mm broad) now accompanying the CAS label (Groves, in litt., October 7, 1992). According to Groves (1992), the surviving specimen (CAS 23007) "... is actually a beachworn *B. alisonae*." Cate (1969) also figured one of two specimens (AMNH

204594) collected at Clipperton Island by Conrad Limbaugh as *B. rashleighana*, but both of these are now also considered to be *B. alisonae* (see Groves, 1992). On the basis of the available data, we delete *B. rashleighana* from the faunal list of the eastern Pacific. This taxon may be a Hawaiian Archipelago endemic (cf. Kay, 1979; Burgess, 1985).

The sole record for the western Atlantic cypraeid *Erosaria spurca acicularis* in the eastern Pacific is based on a single dead specimen collected in April 1992 at Wafer Bay, Cocos Island (Groves, 1992) in the presence of the junior author. Its correct identity was verified shortly after its collection, and this specimen is not to be confused with *Erosaria cernica* (Sowerby, 1870), a widespread Indo-Pacific taxon. The occurrence of this Caribbean subspecies on Cocos Island, if documented by additional collecting, would indicate a disjunct distribution in the eastern Pacific for a western Atlantic emigrant. Another Caribbean species, *Tegula maculostriata* (C. B. Adams, 1845) has long been known from this island (Pilsbry & Vanatta, 1902; Keen, 1971). Furthermore, the shallow-water fauna of Cocos Island shares numerous cognate molluscan species with tropical elements in the western Atlantic (Hertlein, 1963; Montoya, 1983). However, it is the opinion of the junior author that this cowrie was introduced to Cocos Island from a passing vessel. The specimen was collected from scattered dead shell rubble, on sand, in Wafer Bay, precisely at the principal anchorage for yachts and other vessels visiting the island. It is believed that this specimen originated in the Caribbean, was transported through the Panama Canal on a Pacific bound vessel, and was discarded at Cocos Island as an unwanted souvenir.

Although *E. spurca acicularis* is known from the early Neogene of the Caribbean region (Dolin, 1991; Baitoa Formation of the Dominican Republic), and could have conceivably reached the eastern Pacific prior to the closure of the Central American seaways, there is no evidence of its presence in Western Panama despite intensive collecting over the past few years. Until additional specimens are collected at Cocos Island or elsewhere in the region, this record is rejected as being an artifact of human introduction.

Sporadic Immigration

The probability of the recent appearance of *L. lynx* in the eastern Pacific as an isolated immigrant highlights the transitory nature of occurrences for almost all of these cypraeid species. With the exception of *B. alisonae* (= *B. teres* ?), which has been collected during successive years at Cocos Island and is quite widespread and abundant in western Panama (at least in recent years), every other Indo-Pacific cowrie has been sporadically collected either in very limited numbers or as beachworn, single specimens and not consistently over successive years as one would expect from temporally stable populations.

The erratic nature of Indo-Pacific emigration into the

eastern Pacific has been described by numerous workers (Emerson, 1991; Finet, 1991; Kay, 1991; Richmond, 1990; Vermeij, 1978, 1990) as has the role the El Niño/Southern Oscillation phenomenon plays in these events. Our findings reinforce these views.

The role played by periodic occurrences of the El Niño phenomenon on the distributional patterns of Indo-Pacific molluscan species in the eastern Pacific has thus far only been characterized by collection records. In most cases, these records are not of consistent sampling by successive year or season, but rather reflect random collection opportunities. One instance of sequential collection surveys has been at Cocos Island (1982–1992) where *E. caputserpentis* and *M. moneta* were found during the aftermath of the severe El Niño episode of 1982–1983. During subsequent survey trips to Cocos Island in 1987, 1989, 1991, and 1992, no additional specimens of either species were collected. During 1992, the water temperatures at Cocos Island were again substantially elevated as a result of an El Niño which affected the entire region. After this latest event, the first records of occurrence from the west American mainland (Panama) of *M. moneta* (live taken on 12 March 1993; [AMNH 226466]) and *L. lynx* (see above), were reported (Emerson, 1993; Chaney, 1993).

A similar relationship between the occurrence of an El Niño and the appearance of Indo-Pacific species in the Galapagos Islands was reported by Kay (1991). She noted that 16 of her 20 records of Indo-Pacific fauna occurred in or within a year after an El Niño episode.

We suggest that immigrating larvae of these Indo-Pacific cypraeids are able to disperse and successfully settle in the eastern Pacific during the warm-water conditions of an El Niño episode. While they subsequently can grow to maturity, they are unable to successfully reproduce during the normal, cooler water regime and thus eventually die off without progeny. Clearly this process requires more study, particularly by noting survival rates of these introduced species and their fecundity. This cyclical pattern of arrival, maturity without reproduction, and then localized extinction can explain the temporally patchy distribution of many of these taxa (cf. Richmond, 1990). However, this cycle is by no means consistent for all of these Indo-Pacific mollusks. At Cocos Island two of the more common Indo-Pacific gastropods are *Terebra maculata* (Linnaeus, 1758) and *Conus tessulatus* Born, 1778, which have been found in all growth stages and local temperature conditions and appear to be well established.

In summary, the cypraeid gastropods living in the eastern Pacific are a group predominantly composed of temporally established populations of Panamic faunal constituents on the mainland, several of which are recorded from regional Plio-Pleistocene deposits. These Panamic species are also strongly represented in the Galapagos Islands, where two species are known from the fossil record. The Panamic element is weakly represented on Clipperton Island and in the Revillagigedo Islands, but it is moderately represented at Cocos Island. Although they are more di-

verse than the Panamic element, the Indo-Pacific faunal species are largely represented by apparently temporally unstable populations on the oceanic islands (with exception of the Revillagigedo Islands which lacks this element). Only one Indo-Pacific species (*Blasicrura alisonae* [= *B. teres*?]) appears to be temporally established on the mainland. Additional fieldwork will be required to substantiate our preliminary conclusions pertaining to the questionable stability of the populations of the Indo-Pacific cypraeid species in this region. It is also clear that the list of immigrant species will continue to grow as future collecting surveys are conducted.

ACKNOWLEDGMENTS

We are pleased to acknowledge with thanks the cooperation of a number of people for their aid in the completion of this paper. Type and other specimens and/or locality data were provided by Gary Rosenberg and Doree Bardes (ANSP), Terrence M. Gosliner and Robert Van Syoc (CAS), Fred G. Thompson and Kurt Auffenberg (FMNH), James H. McLean and Lindsey T. Groves (LACM), David R. Lindberg and Carole S. Hickman (MPB), Alison Trew (NMW), Regina Wetzer (SDNHM), M. G. Harszewych and Raye N. Germon (USNHM), Hugh Bradner (La Jolla, California), Donald R. Shasky (Redlands, California), Kirstie L. Kaiser (Salt Lake City, Utah) and John D. Jackson (El Cajon, California). Hugh Bradner, Lindsey T. Groves, E. Alison Kay (University of Hawaii, Honolulu, Hawaii), and Doug von Kriegerstein (Loma Linda, California) provided information on critical specimens. Laura Sarti M. and Tangaxoan Argueta (Departamento De Biologica, Universidad Nacional de México, Mexico D.F.) generously collected and donated specimens of mollusks from Socorro Island, Revillagigedo Islands as part of their ongoing field studies; René Martínez Tinajero (Guadalajara, Mexico) assisted in expediting the collection of these mollusks. We are also indebted to our colleagues at the AMNH, Walter E. Sage, III for technical assistance, Andrew S. Modell for photographic services, and Stephanie Crooms and Barbara Worcester for word processing the manuscript. We thank Lindsey T. Groves and Geerat Vermeij for critically reviewing the manuscript and offering helpful suggestions.

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An Early Oligocene Chemosynthetic Community from the Makah Formation, Northwestern Olympic Peninsula, Washington

by

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Abstract. A small, allochthonous, localized mass of limestone is present within deep-water strata of the early Oligocene part of the Makah Formation exposed at Shipwreck Point on the Olympic Peninsula, Washington State. This limestone is a methane-derived authigenic carbonate, as evidenced by faunal-sedimentologic associations and stable isotopes; it is enclosed in siltstone that is nearly barren of megafossils. Fossils from the limestone represent a diverse chemosynthetic community that includes more than 20 species. The fauna consists of eight bivalve genera (including *Calyptogena* and *Modiolus*), 13 gastropods (including *Provanna*), one scaphopod, one chiton, and vestimentiferan? worm tubes. We report the first fossil record for the genus *Provanna* and the first record for chitons at ancient cold-methane seeps.

INTRODUCTION

Fossil communities of chemosynthetically-supported mollusks similar to those now living near modern hydrothermal vents and cold-seeps have now been recognized in rocks around the world. Ancient cold-seeps have been described from marine sedimentary deposits in Europe (Gaillard et al., 1985; Clari et al., 1988); Japan (Niitsuma et al., 1989); the Canadian Arctic (Beauchamp et al., 1989); and the western United States (Howe & Kauffman, 1986; Campbell, 1989, 1992; Goedert & Squires, 1990; Campbell & Bottjer, 1993). Most of these reports discuss stratigraphic, petrographic, and isotopic data from suspected seep sites, with the faunas only briefly mentioned.

The purpose of this paper is to document a newly discovered Oligocene cold-seep fauna from localized limestone within deep-water sandstone and siltstone deposits in the

Makah Formation at Shipwreck Point, northwestern Olympic Peninsula, Washington (Figure 1). All the taxa are illustrated except those recently described from other known ancient cold-seep faunas or too poorly preserved for identification. Some of the mollusks from this fauna are new species, and will be described by others. The acronym LACMIP designates catalog and locality numbers of the Natural History Museum of Los Angeles County, Invertebrate Paleontology Section, Los Angeles, California. Locality LACMIP 15911 is an isolated *in situ* limestone block (2.5 m long × 2.5 m wide × 0.75 m high), accessible only during low tides (Figure 1). Locality LACMIP 8233 represents float, erosional-lag materials, on the modern beach terrace. Rare limestone blocks up to 1 m across are present on the beach terrace. They are more weathered and easier to sample for fossils than the *in situ* block (LACMIP loc. 15911), and most of the specimens

illustrated were obtained from them. The loose, smaller blocks of limestone are identical to the *in situ* block, and all taxa found in the smaller blocks were also found in the *in situ* block. Approximately 200 kg of limestone were sampled for fossils.

DEPOSITIONAL ENVIRONMENT AND AGE

The Makah Formation was deposited in a deep-water, submarine-fan setting, and is late Eocene to late Oligocene in age (Snively et al., 1980). It contains six named members: four are thick turbidite sandstones; a fifth (the Jansen Creek Member) is made up of olistostromal and deformed shallow-water strata; and a sixth unit is a thin tuff deposit. Thin-bedded sandstones and siltstones separate each member and represent basin-plain and outer fan-fringe deposits (Snively et al., 1980). Limestones are isolated and rare both in the Makah Formation and in other Cenozoic, deep-water siliciclastic sequences throughout the Pacific Northwest.

The *in situ* limestone (LACMIP loc. 15911) is positioned stratigraphically within the basin-plain and fan-fringe deposits of the Makah Formation. A 10 cm-thick turbidite sandstone bed is preserved 2.5 m stratigraphically below the limestone. The surrounding siltstone is barren of megafossils and contains scattered calcareous concretions, a few small blocks of sandstone, glauconitic siltstone horizons, and oblong concretionary blocks that are oriented randomly with respect to bedding. Based on the following evidence, we conclude that the limestone originally formed in a shelf/slope environment and subsequently slid or slumped into mid to lower bathyal parts of a basin. First, the Jansen Creek Member of the Makah Formation is located only about 30 m stratigraphically below the *in situ* limestone. The Jansen Creek Member is an olistostromal unit (200 m thick), derived from shallow- and deep-water sediments that slumped or slid off the Vancouver Island shelf/slope into a deep marginal basin (Snively et al., 1980; Niem et al., 1989). Second, petrographic observations on micritic limestone from the *in situ* block yielded a probable nodosariid microfossil (A. G. Fischer, personal communication). Nodosariids are typically associated with outer shelf to bathyal water depths (Boersma, 1978); therefore, its presence within a limestone block surrounded by mid to lower bathyal strata may imply an allochthonous origin. Third, the contact between the limestone and the enclosing siltstone is sharp. Ancient cold-seep limestone mounds that formed *in situ*, due to concentrated fluid seepage, typically preserve nodular carbonate material trailing into the siliciclastic deposits around all the mound margins (Rolin et al., 1990).

The upper part of the Makah Formation in the vicinity of Shipwreck Point is early Oligocene in age (Snively et al., 1980). This age assignment is based on benthic foraminifera; molluscan fossils are rare in the basin-plain deposits. This part of the Makah Formation also contains rare fossils of isopod crustaceans (Wieder & Feldmann,

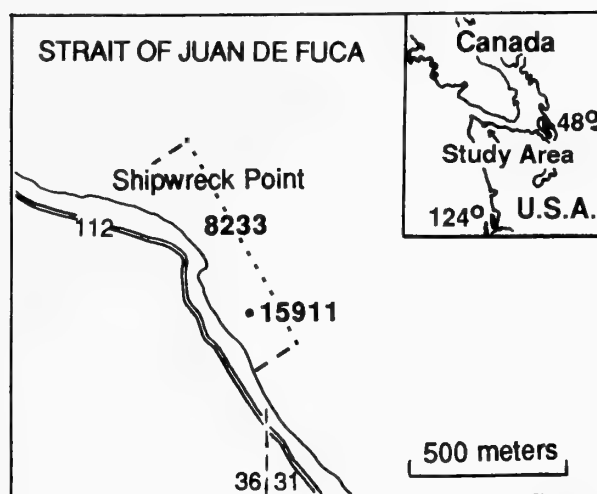


Figure 1

Index map of Shipwreck Point, Washington showing fossil localities.

1989), a few mollusks associated with cetacean skeletons and pieces of wood (Squires et al., 1991), and a few bivalves associated with turbidite deposits (Goedert & Squires, 1993). The limestone (LACMIP loc. 15911) at Shipwreck Point differs from the nearly barren surrounding siltstone in that it contains an abundance of fossil invertebrates, all randomly oriented and, in places, closely packed together. For this diverse, localized assemblage (Table 1) we apply the term "community" defined by Hickman (1984:1220) as "an association of organisms inferred to have lived together and interacted ecologically." Nearly identical Eocene-age localized carbonate deposits from southwest Washington contain faunas interpreted by Goedert & Squires (1990) as representing chemosynthetic communities formed near cold-seeps in deep water. Similar isolated limestones in deep-water siliciclastics have been recognized as additional cold-seep sites in various sedimentary sequences in the Pacific Northwest Cenozoic and California Mesozoic (Campbell, 1989, 1992; Campbell & Bottjer, 1993).

PETROGRAPHY AND STABLE ISOTOPES

The petrographic and stable-isotopic signatures of several representative carbonates from the Shipwreck Point area reveal microenvironmental details of the seep-origin of the limestone. The *in situ* block (LACMIP loc. 15911) has both micritic and layered-calcite cement fabrics. The smaller blocks (LACMIP loc. 8233) show either micritic fabrics or layered-calcite cement fabrics. Fossils are rare to absent in the blocks composed of layered-calcite cements but are more common in the indurated micritic limestone. A similar association between micrite/calcite cement fabrics and faunal distributions has been observed for Jurassic and

Table 1

Megafossil assemblage from isolated limestone within the Makah Formation at Shipwreck Point, Washington (listed in order referred to in text).

Bivalves	
<i>Modiolus (Modiolus) willapaensis</i>	Squires & Goedert
<i>Calyptogena (Calyptogena) chinookensis</i>	Squires & Goedert
<i>Acharax</i>	sp.
<i>Anodontia?</i> (<i>Anodontia?</i>) <i>inflata</i>	(Wagner & Schilling)
<i>Lucinoma hannibali</i>	(Clark)
Unidentified lucinid	
<i>Nuculana</i>	sp.
<i>Macoma?</i>	sp.
<i>Vesicomya?</i>	sp.
Gastropods	
<i>Provanna</i>	n. sp.
" <i>Admete</i> "	n. sp.
<i>Margarites (Pupillaria) columbiana</i>	Squires & Goedert
Hyalogyrinids (2 spp.)	
Limpet	
<i>Solariella?</i>	sp.
<i>Aforia</i>	sp.
Naticids	
Marginellids	
Scaphandrids	
Turrid	
Buccinid	
Polyplacophoran	
<i>Leptochiton</i>	sp.
Other	
Scaphopod	
Vestimentiferan? worm tubes	
Shrimp, <i>Callinassa</i> sp.	

Cretaceous seep limestones in California (Campbell, unpublished data).

Several representative thin-sections of carbonate were cut from the *in situ* block to be examined petrographically. It is composed predominantly of a dark gray-brown lime mudstone or micrite, containing abundant quartz and feldspar grains and woody debris. Relatively homogeneous regions of micrite are commonly disrupted by irregular intraclasts of micrite with diffuse boundaries, or by angular to rounded, brecciated micrite fragments. Fibrous cements and blocky, clear spar fill pore spaces between micrite fragments, but the micrite/cement ratio is high.

Pyrite-coated corrosion surfaces are prevalent in some of the micritic thin-sections and in places, pyrite is interlayered with micrite on a fine-scale. Some modiolid bivalves are also coated with a thin layer of pyrite, but the underlying calcareous shell layers remain unaffected by pyritization. Some of the woody debris has been replaced by pyrite. Pyrite coatings and corrosion surfaces reported from several ancient cold-seep settings probably represent phases of sulfide-rich fluid seepage in a locally geochem-

ically reduced seep-microenvironment (Beauchamp & Svard, 1992; Campbell et al., 1993).

Two carbonate and two fossil shell samples from the *in situ* block (LACMIP loc. 15911) were examined isotopically (Table 2). Carbonate components were separated with a microdrill, weighed (150–400 μg); and roasted *in vacuo* at 375°C for one hour. $\text{CO}_2(\text{g})$ was devolved from the sample by reaction in orthophosphoric acid at 90°C. Weighed standards (Ultissima marble) were interspersed with samples and analyzed under the automated runs. Isotopic signatures of shell material can be compared to modern seawater values ($\sim 0\text{‰}$ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, PDB [Hoefs, 1987]), with slight isotopic enrichment in carbon values and slight isotopic depletion in oxygen values for the sampled fossil solemyid. These results fall in the range of shell carbonate values reported from both littoral and vent/seep modern bivalves, albeit chemosynthetic taxa tend to show either more depleted (to -6‰) or more positive (to $+4\text{‰}$) $\delta^{13}\text{C}$ signatures (Rio et al., 1986, 1992). Fibrous cements are depleted in carbonate carbon (to -34‰), suggesting that methane was present in fluids that precipitated the cements (see Anderson & Arthur, 1983). It is unknown whether thermogenic or biogenic sources were tapped, or if mixing with other carbon reservoirs affected the isotopic signal. For example, typical carbon sources for most deep-sea settings include: total dissolved inorganic carbon in seawater (0‰); marine organic carbon, particulate and dissolved (~ -20 to -25‰); terrestrial plant material (~ -10 to -30‰); thermogenic methane (+ values to -40‰); and biogenic methane (~ -50 to $< -80\text{‰}$) (Paull et al., 1985, and references therein). Oxygen isotopic signatures of the cement are consistent with seawater values and indicate that there was no significant change in ambient temperature of formation. Additional isotopic measurements are needed to more clearly elucidate these relationships and to ascertain the origin of the micrite.

PALEONTOLOGY

In the fossiliferous micritic limestone at Shipwreck Point, the most common faunal constituents are the bivalves *Modiolus (Modiolus) willapaensis* Squires & Goedert, 1991, from 4 to 27.9 mm in length, and *Calyptogena (Calyptogena) chinookensis* Squires & Goedert, 1991, up to 33 mm in length. Most specimens are articulated, in some cases in clusters of randomly oriented individuals. Both of these bivalves have been reported from cold-seep limestones in southwestern Washington. *Calyptogena (Calyptogena) chinookensis* has also been reported from cold-seep limestone of Oligocene age in the Pysht Formation about 50 km southeast of Shipwreck Point and in turbidites from below the Jansen Creek Member of the Makah Formation (Goedert & Squires, 1993).

Most of the micritic limestone contains angular, unworn fragments of the bivalve *Acharax* sp.; however, one poorly preserved, articulated specimen from a block of layered-calcite crusts is 75 mm long and 35 mm high. This block

also contained sparse specimens of *Modiolus* (*Modiolus*) *willapaensis*.

The limestone also contains poorly preserved bivalves that resemble *Thyasira*, but may be *Anodontia*? (*Anodontia*?) *inflata* (Wagner & Schilling, 1923), known previously only from Eocene rocks in California (Moore, 1988). The hinge is not exposed in any of the Shipwreck Point specimens, but some show faint irregular internal ribbing. They are found articulated and as single valves and are from 7.6 up to 48 mm in length.

Specimens of *Lucinoma hannibali* (Clark, 1925) are rare in the limestone; all are articulated and are from 7.8 to 31.9 mm in length. Fragments of another, unidentified lucinid bivalve were also found; if complete, its length would exceed 75 mm. Single and articulated valves of a rare, small species of *Nuculana* (up to 7 mm length) are also present. The shell of *Nuculana* sp. (Figure 2) has numerous well-defined concentric ribs on the posterior and mid-sections, but the anterior third is always smooth. Two specimens of *Macoma*? sp., length 14.5 to 18.5 mm, were also found; one was associated with numerous specimens of articulated and randomly oriented *Calypptogena* (*Calypptogena*) *chinookensis*.

A single valve of *Vesicomya*? sp. (Figure 3) was also found in the limestone. The hinge is not exposed, but the valve is referred to *Vesicomya* because of the strongly curved beak, smooth and extremely convex shell, lunule with a groove, slight depression posteriorly, and general outline of the shell.

Gastropods are abundant in the limestone that contains bivalves, but most of the gastropods are quite small. One new species, or possibly more, of the genus *Provanna* are present (Figures 4–7), ranging from about 2 to 7 mm in height (under study by R. L. Squires). Some have a smooth shell (Figure 4), somewhat like the modern *Provanna laevis* Warén & Ponder, 1991. A few specimens have spiral ribs (Figures 5, 6) and resemble some specimens of the modern *Provanna macleani* Warén & Bouchet, 1989, and some also have axial ridges (Figure 7). The apex is not present in any of the *Provanna* specimens, probably due to corrosion during life. *Provanna* has no previously documented fossil record, and almost all living species are thought to be from hydrocarbon seeps or hydrothermal vents (Warén & Bouchet, 1986, 1989; Warén & Ponder, 1991).

Another gastropod in the limestone is "*Admete*" n. sp. (Figure 8). Specimens are moderately common and range in height from 5 to 17 mm. "*Admete*" n. sp. resembles "*Admete*" *umbilicata* Hickman, 1980, from bathyal rocks in the late Eocene and early Oligocene Keasey Formation in northwest Oregon, but "*Admete*" n. sp. is more elongate with more steeply inclined whorls.

Five specimens of *Margarites* (*Pupillaria*) *columbiana* Squires & Goedert, 1991, were found and range from 5.1 to 9.6 mm in height. This species had previously been found in only one other cold-seep fauna in late Eocene rocks in southwestern Washington (Squires & Goedert, 1991).

Table 2

Carbon and oxygen isotope values from representative Shipwreck Point fossil shells and carbonate fabrics. See text for interpretation.

Material	$\delta^{13}\text{C}$ (‰)	$\delta^{18}\text{O}$ (‰)
Solemyid shell, umbo, outer shell layer	2.06	-1.76
Solemyid shell, posterior, inner shell layer	2.46	-1.12
Fibrous cement	-26.20	-2.29
Fibrous cement	-34.47	-0.76

Delta (δ) values are given in per mil (‰), such that $\delta^{13}\text{C} = [(^{13}\text{C}/^{12}\text{C})_{\text{sample}} \div (^{13}\text{C}/^{12}\text{C})_{\text{standard}} - 1] \times 1000$ (‰), where standard = Pee Dee Formation belemnite (PDB). Same notation and form applicable to oxygen-isotope data. The precision of measurements is better than 0.1‰.

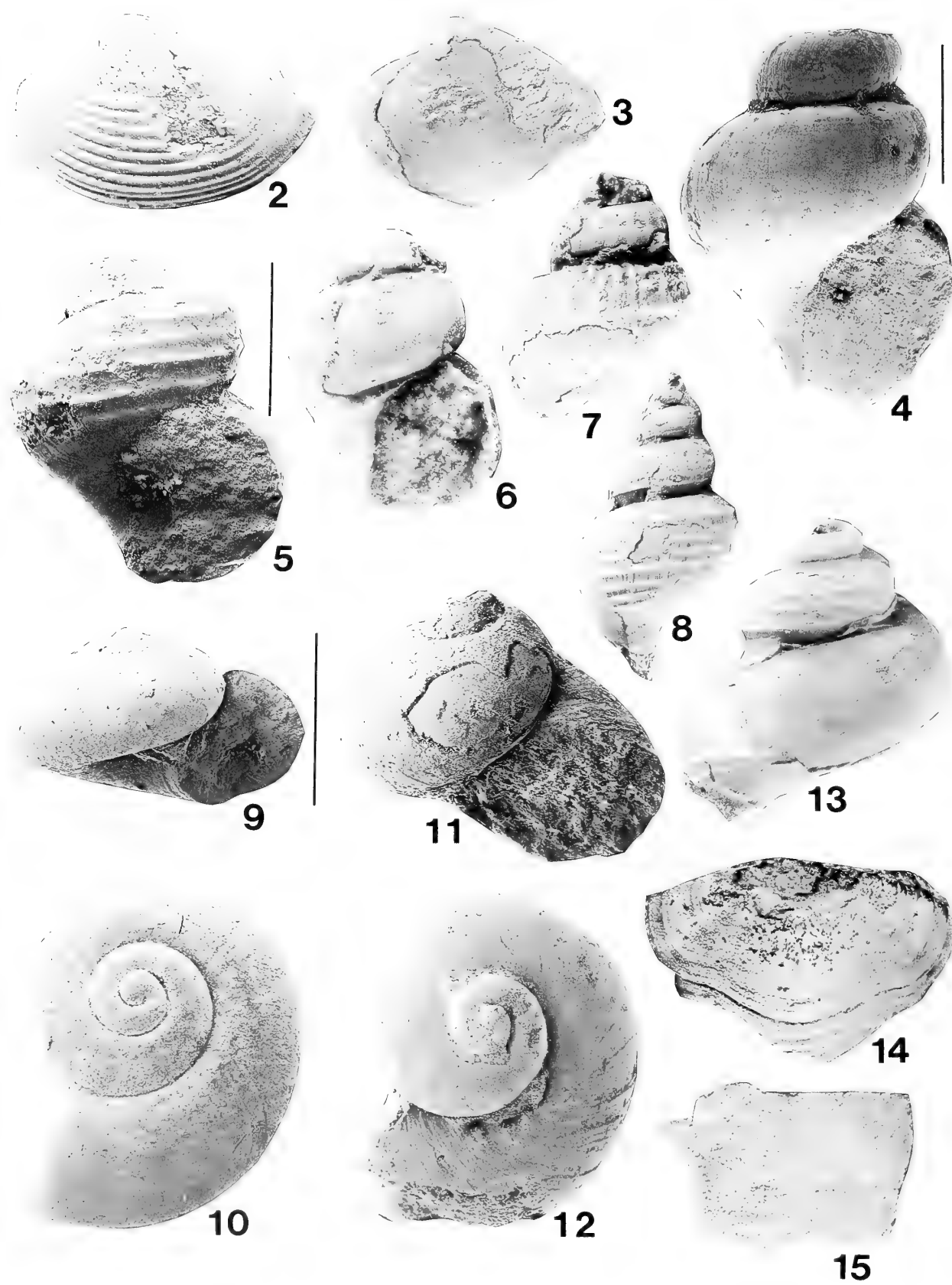
The limestone contains numerous specimens of unidentified, minute gastropods (Figures 9–12), which are probably species belonging to the family Hyalogyrinidae Warén & Bouchet, 1993. One species is about 1 to 2 mm in diameter, and some specimens have the larval shell intact (Figures 9, 10). Another species has a higher spire, more fragile shell, and is 2 to 4 mm in height (Figures 11, 12). Living hyalogyrinids are usually found in deep water, associated with sunken organic debris or hydrothermal vents (Marshall, 1988; Warén et al., 1993).

Three minute limpets found in the limestone have smooth shells, 1 to 2 mm in diameter, and are identical to the limpet reported (Goedert & Squires, 1990:1184, fig. 2b, c) from the cold-seep community in the middle to upper Eocene Humptulips Formation in southwest Washington. This limpet has also now been collected in the upper Eocene Bear River cold-seep limestone in Pacific County, Washington (Goedert, unpublished data).

At least seven other gastropod species are present in the limestone but are poorly preserved. A single, incomplete specimen of *Solariella*? sp. (Figure 13), one specimen of a small *Aforia* sp., five specimens of an unidentified naticid, three specimens of a marginellid, one scaphandrid, and one turrid gastropod were found. Four specimens of a buccinid up to 23.5 mm in height were also found.

Chiton plates (Figures 14, 15) are common in the limestone. They are small and represent a species of *Leptochiton* Gray, 1847. Some modern species of *Leptochiton* are found in deep water (Ferreira, 1981). Unidentified chitons have been reported associated with authigenic carbonates in shelf/slope environments off the Oregon coast (Kulm & Suess, 1990).

Other invertebrates found in the limestone are poorly preserved. Echinoid spines are commonly visible in thin-sections. A single unidentifiable scaphopod was found. Individual tubes of vestimentiferan? worms are thin-walled and up to 2.9 mm in diameter. Fragments of crustaceans



probably represent a species of the shrimp *Callinassa* (R. B. Manning, personal communication).

Small fragments of woody detritus are sparse throughout the limestone. A single fossil seed was found (Florida Museum of Natural History UF12745) and identified as *Cruciptera* sp. (S. R. Manchester, personal communication). This genus has been identified in terrestrial deposits of Eocene and Oligocene age in Oregon, Washington, and Wyoming, and middle Eocene rocks in England and Germany (Manchester, 1991).

DISCUSSION

The fossil mollusks contained within the Shipwreck Point limestone are typical of taxa described from modern and ancient hydrothermal vent and cold-seep settings, both in terms of abundance and dominant genera. The limestone contains numerous macroinvertebrates whereas the surrounding basin-plain deposits are nearly barren. Modern deep-sea vent/seep communities owe their extraordinary population densities to the geochemical food base exploited by chemoautotrophic bacteria (free-living and endosymbiotic) which rely on localized, reduced fluid seepage. Moreover, the dominant fossil genera collected from the limestone include *Modiolus*, *Calyptogena*, and *Provanna*; and all have species known today to be chemosynthetic. Other vent/seep taxa are also well represented; solemyid and lucinid bivalves, the gastropod genus *Margarites*, hyalogyrinid gastropods, limpets, and tubes of vestimentiferan? worms. Overall, the macroinvertebrate fossil assemblage from Shipwreck Point represents a relatively diverse chemosynthetic community. This is a significant finding because, by contrast, most reported chemosynthetic communities (modern and ancient) show relatively low species richness; however, most have been poorly sampled.

The association of vent/seep-type taxa with anomalous, isolated carbonates that have peculiar sedimentologic and isotopic characteristics is typical for modern and ancient cold-seep environments thus far recognized. This faunal-sedimentologic association allows for prediction of new sites, both in modern settings and in the geologic record, and enables identification of the local geochemical condi-

tions necessary for chemosynthetic taxa to flourish. For example, studies of modern and ancient seep-carbonates show that they are derived from the oxidation of methane, mixed to varying degrees with seawater (Ritger et al., 1987; Han & Suess, 1989; Campbell, 1992). Depleted $\delta^{13}\text{C}$ signatures from two cement samples from Shipwreck Point also suggest that methane was present during carbonate formation. Modiolids, present in abundance in the limestone, rely today on methane for chemosynthesis. Furthermore, pyrite-coated corrosion surfaces in the micrites attest to the presence of sulfide-rich fluids in the depositional environment, a necessary component to chemosynthesis for the solemyids, vesicomyids, and vestimentiferan worms.

The tectonostratigraphic conditions that allowed formation of the Shipwreck Point cold-seep deposit included: (1) generation and migration of reduced fluids (methane and hydrogen sulfide) to the sea-floor owing to convergent margin tectonism; (2) carbonate formation contemporaneous with seep community development around seep effluent area; and (3) slumping/sliding of this outer shelf or slope-derived limestone into mid to lower bathyal depths where the Makah Formation accumulated. The allochthonous nature of the Shipwreck Point limestone block is peculiar to this locality; most other reported ancient seep-carbonate deposits from western North America are preserved in place, in outer shelf to slope paleoenvironments (Campbell & Bottjer, 1993).

ACKNOWLEDGMENTS

We thank Richard L. Squires (California State University, Northridge) and Alicia Thompson (USC, Center for Electron Microscopy and Microanalysis) for assistance with photography of specimens for this study and Robert B. Manning (U.S. National Museum), William A. Newman (Scripps Institution of Oceanography), and Steven R. Manchester (Florida Museum of Natural History) for help in identifying fossils. For comments on the manuscript we thank Ellen J. Moore, Barry Roth, Richard L. Squires, and an anonymous reviewer. Thomas E. Angelos read the manuscript. Gail H. Goedert and William R. Buchanan

Explanation of Figures 2–15

All specimens from limestone blocks at LACMIP loc. 8233 unless otherwise noted. Scale line for SEM photos is 1 mm. Figure 2. *Nuculana* sp., LACMIP 12310, right valve, $\times 7.4$. Figure 3. *Vesicomya*? sp., LACMIP 12311, Loc. LACM 15911, right valve (convexity 4.8 mm), $\times 3.3$. Figures 4–7, *Provanna* (one, or possibly more n. sp.). Figure 4. LACMIP 12312, apertural view, SEM. Figure 5. LACMIP 12313, apertural view, SEM. Figure 6. LACMIP 12314, apertural view, $\times 10.5$. Figure 7. LACMIP 12315, back view, $\times 7$. Figure 8. "*Admete*" n. sp., LACMIP 12316, back view, $\times 3.3$. Figures 9, 10. Hyalogyrinid, LACMIP 12317, SEM. Figure 9. Apertural view, Figure 10. Dorsal view. Figures 11, 12. Hyalogyrinid, SEM (same scale as Figure 9). Figure 11. LACMIP 12318, oblique-apertural view, Figure 12. LACMIP 12319, dorsal view. Figure 13. *Solariella*? sp., LACMIP 12320, LACMIP loc. 15911, back view, $\times 3.7$. Figures 14, 15. *Leptochiton*? sp. Figure 14. Intermediate valve (anterior end toward bottom of page), LACMIP 12322, dorsal view, $\times 7.6$. Figure 15. Fragment of intermediate valve, LACMIP 12321, dorsal view, $\times 9.25$.

helped at various times with fieldwork. Fieldwork by James L. Goedert was supported by a National Geographic Society grant (4439-90) to the Natural History Museum of Los Angeles County Foundation, for research on fossil cetacea on the Olympic Peninsula, Washington. Isotopic analyses were performed with the assistance of Ashish Sinha in the laboratory of Lowell D. Stott, University of Southern California. Research by Kathleen A. Campbell was supported by the donors of the Petroleum Research Fund, administered by the American Chemical Society.

LOCALITIES CITED

LACMIP loc. 8233. Float eroded from bedrock exposed on modern beach terrace at Shipwreck Point, SE¼ NE¼ sec. 36, T. 33 N, R. 14 W, (U.S. Geological Survey, 7.5-minute, Sekiu River, Washington quadrangle, provisional edition 1984) Clallam County, Washington. Upper part of Makah Formation. Age: Early Oligocene.

LACMIP loc. 15911. *In situ* isolated limestone block within thin-bedded sandstone and siltstone deposits, about 30 m stratigraphically above top of Jansen Creek Member, block measures 1.5 m (N-S) by 2.5 m (E-W), and is weathered out 0.75 m higher than surrounding siltstone; accessible only at low tide. Block is approximately 175 m southeast of tip of Shipwreck Point, SE¼ NE¼ sec. 36, T. 33 N, R. 14 W, (U.S. Geological Survey, 7.5-minute, Sekiu River, Washington quadrangle, provisional edition 1984) Clallam County, Washington. Upper part of Makah Formation. Age: Early Oligocene.

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First Fossil Species of the Chemosynthetic-Community Gastropod *Provanna*: Localized Cold-Seep Limestones in Upper Eocene and Oligocene Rocks, Washington

by

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Abstract. The only known fossil species of the chemosynthetic-community gastropod *Provanna* is named and described from four localized Eocene and Oligocene cold-seep limestones in western Washington. The new species, *Provanna antiqua*, is present in the upper Eocene Bear River deposit near the mouth of the Columbia River, in the lower Oligocene Makah Formation at both Shipwreck Point and near Neah Bay on the northern Olympic Peninsula, and in the upper Oligocene part of the Lincoln Creek Formation at Canyon River in southwestern Washington. The deep-sea limestones at these localities contain dense concentrations of macrobenthos that lived in association with subduction-related cold-methane seeps.

Provanna antiqua shows a great range in shell morphology, from smooth to moderately sculptured to cancellate, and there can be as much variation on a single specimen from whorl to whorl as in the whole material. The morphologic variation of the new species is very similar to that in specimens of modern *P. variabilis*.

INTRODUCTION

Most modern species of the gastropod genus *Provanna* Dall, 1918, are associated with chemosynthetic, sulphide-rich environments of the deep sea where there is hydrothermal activity or hydrocarbon seepage (Warén & Ponder, 1991; Lutz, 1991–1992; Tunnicliffe, 1992). At each chemosynthetic biotope, *Provanna* is usually represented by one or two species (Warén & Bouchet, 1993). Recently, the first fossil occurrence of *Provanna* was reported by Goedert & Campbell (1995) who discovered specimens in a cold-methane-seep community of early Oligocene age in Washington. The purpose of this paper is to describe and name this fossil species of *Provanna*. In addition, three other localities for this new species are reported from other cold-methane-seep chemosynthetic communities in localized limestones in lower Tertiary rocks in Washington.

Abbreviation used for catalog and/or locality numbers is: LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

STRATIGRAPHIC DISTRIBUTION AND GEOLOGIC AGES

Goedert & Campbell (1995) reported morphologically variable specimens of *Provanna* sp. in a cold-seep limestone block at LACMIP loc. 15911 in the Makah Formation at Shipwreck Point, northern Olympic Peninsula, Washington (Figure 1). The Makah Formation was most likely deposited in a bathyal, submarine-fan setting (Snively et al., 1980). The Jansen Creek Member of the Makah Formation is only about 30 m below the limestone block. This member is a transported olistostromal unit containing mostly shallow-water marine conglomerate and fossiliferous sandstone that slid into the basin in which the Makah Formation was being deposited and became enclosed in deep-water (1000 to 2000 m) marine siltstone sandstone (Snively et al., 1980; Kaler, 1988). Goedert & Campbell (1995) concluded that the limestone block at Shipwreck Point is also allochthonous. The limestone is about one meter thick and is highly fossiliferous with randomly ori-

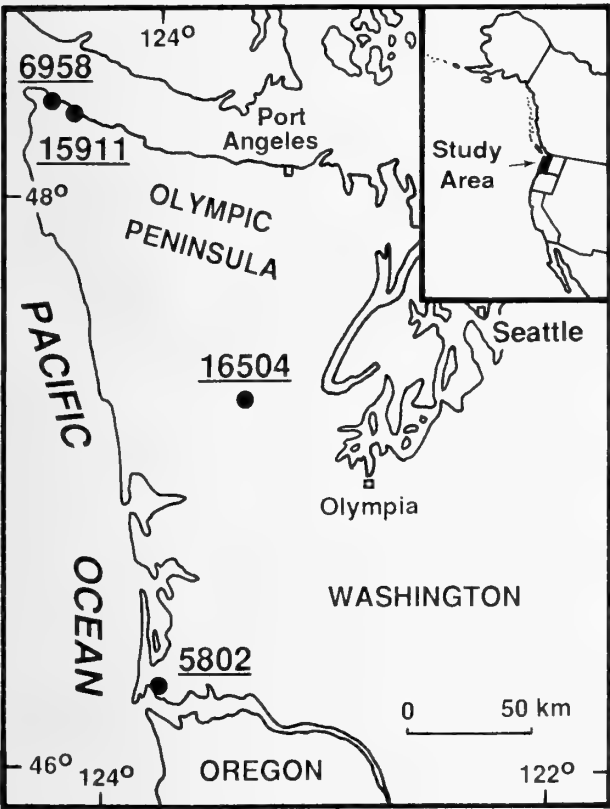


Figure 1

Index map to localities of *Provanna antiqua* Squires, sp. nov.

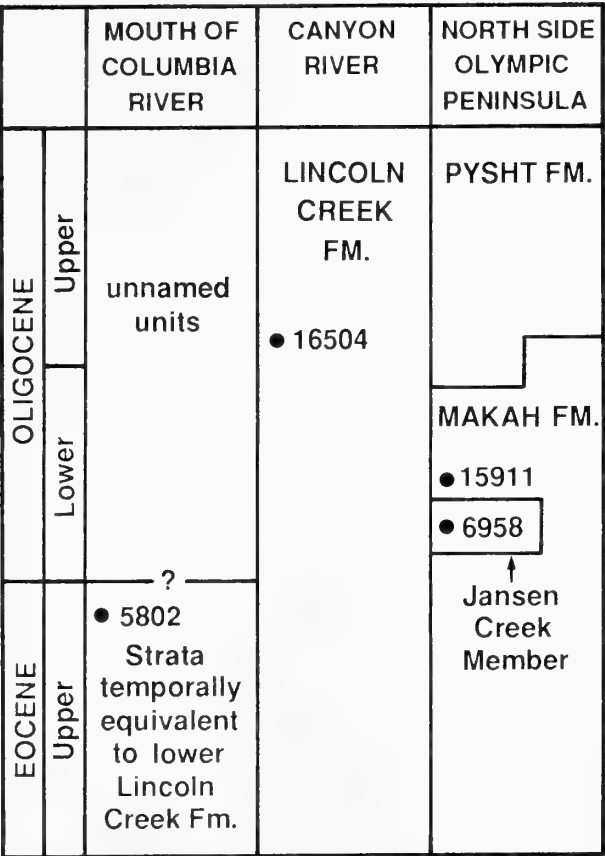


Figure 2

Chronostratigraphic chart showing position of localities for *Provanna antiqua* Squires, sp. nov.

ented specimens that are, in places, closely packed together. They reported that the bivalves (*Modiolus (Modiolus) willapaensis* Squires & Goedert, 1991, and *Calyptogena chinookensis* Squires & Goedert, 1991 are abundant and are associated with vestimentiferan(?) worm tubes, chiton plates, scaphopods, many archaeogastropods and other gastropods, other bivalves, crustacean fragments, and wood fragments. The limestone is enclosed in siltstone barren of megafossils. The portion of the Makah Formation that lies stratigraphically just above the Jansen Creek Member is early Oligocene in age (Figure 2) (Armentrout et al., 1983; Hull et al., 1988). Squires & Goedert (1994) also reported an early Oligocene age for this formation in the vicinity of Shipwreck Point.

Approximately 200 kg of limestone was collected by J. L. Goedert at the Shipwreck Point locality. Most is very hard micritic limestone, and the extraction of fossils is difficult. For some specimens, shell material adheres to the matrix and leaves only internal molds for study. Fifty-six specimens of *Provanna* were found, and 47 (84%) have their shell material intact. The only species of *Provanna* at this locality is *Provanna antiqua*, and it shows much morphologic variation.

Recent fieldwork by J. L. Goedert has yielded another

locality in the Jansen Creek Member of the Makah Formation, northern Olympic Peninsula, where *Provanna antiqua* is present. A single specimen of the new species was found at LACMIP loc. 6958 (Figure 1) in an undescribed cold-seep limestone in the lower Oligocene Jansen Creek Member of the Makah Formation (Figure 2).

Additional fieldwork by J. L. Goedert has yielded a third locality where specimens of *Provanna antiqua* are present. Numerous specimens were found at LACMIP loc. 5802 in a localized limestone temporally equivalent to the lower part of the Lincoln Creek Formation at Bear River, near the mouth of the Columbia River, southwestern Washington (Figures 1, 2). The limestone was deposited in a subduction zone where subsurface methane-rich waters discharged onto the ocean floor (Goedert & Squires, 1990). The limestone, which is exposed in an abandoned quarry, is 15 m thick, 68 m in length, and 38 m wide. It is highly fossiliferous with dense concentrations of the bivalves *Modiolus willapaensis* and *Calyptogena chinookensis*. Other fossils are siliceous sponges, serpulid and vestimentiferan(?) worm tubes, scaphopods, archaeogas-

tropods and other gastropods, other bivalves, crustacean parts, wood fragments, and fish bone. Bivalves are articulated and show growth series (Goedert & Squires, 1990). Several of the molluscan species were named and described by Squires & Goedert (1991). The surrounding rock is deep-water siltstone with few megafossils. The limestone is late Eocene in age (Zone CP15b of Okada & Bukry, 1980) based on calcareous nannofossils and benthic foraminifera (Goedert & Squires, 1990).

Extraction of fossils from the limestone at the Bear River locality is more difficult than that for the limestone in the Makah Formation at Shipwreck Point. One hundred and sixty-four specimens of *Provanna antiqua* were found at the Bear River locality, but only 41 (25%) of these had their shell material intact.

Recent fieldwork by J. L. and G. H. Goedert and K. L. Kaler has yielded a fourth locality where specimens of *Provanna antiqua* are present. Numerous specimens were found at LACMIP loc. 16504 in a small cold-methane-seep limestone block in the upper part of the Lincoln Creek Formation at Canyon River, in the Satsop River area, Grays Harbor County, southwestern Washington (Figure 1). The limestone contains numerous specimens of *Provanna antiqua* and a diverse chemosynthetic community. The surrounding rock is sparsely fossiliferous siltstone containing cold-methane-seep limestones with bivalves (*Acharax* sp. and *Thyasira* sp.) (J. L. Goedert, personal communication). These cold-seep limestones are under study by J. L. Goedert and K. L. Kaler. The limestone at LACMIP loc. 16504 is in the vicinity of benthic foraminifera localities F 107 to 110 of Rau (1966) and mollusk localities CR 39–44 of Armentrout (1973). Both of these workers assigned the rocks at their respective localities to the upper Oligocene (= *Echinophoria apta* Molluscan Zone of Durham, 1944). Moore (1963) subsequently assigned the gastropod *E. apta* to genus *Liracassis*. Specimens of a stratigraphically lowest morph of *Liracassis apta* (Tegland, 1931) were found a short stratigraphic distance downsection from LACMIP loc. 16504 (Armentrout, 1973:pl. 6, fig. 10; J. L. Goedert, personal communication), and it is concluded that the rocks at LACMIP loc. 16504 are earliest late Oligocene in age.

The specimens of *Provanna antiqua* at LACMIP loc.

16504 are the best preserved of this species. Many specimens could be completely freed from the matrix. Ninety-six specimens were found, and nearly all have their shell material intact.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Subclass Prosobranchia Milne-Edwards, 1848

Order Caenogastropoda Cox, 1960

Superfamily LOXONEMATOIDEA Koken, 1889

Family PROVANNIDAE Warén & Ponder, 1991

Discussion: In this report, the higher systematics of this family follow that of Warén & Bouchet (1993).

Genus *Provanna* Dall, 1918

Type species: ? *Trichotropis* (*Provanna*) *lomana* Dall, 1918, by monotypy, Recent, off Point Loma at 1183 m depth, San Diego, California.

Discussion: There are currently four genera, including *Provanna*, recognized in the family Provannidae; they are reviewed in Warén & Bouchet (1993). Wenz (1940) reported that *Provanna* is confined to the Recent. There are at least 13 living species of *Provanna*, and most of these are illustrated by Warén & Bouchet (1986) or by Warén & Ponder (1991). Shells of the remaining species are illustrated by Warén & Bouchet (1989), Okutani (1990), or Warén & Bouchet (1993). The latter workers assigned one of Okutani's species of *Provanna* to genus *Desbruyeresia* Warén & Bouchet, 1993.

Provanna antiqua Squires, sp. nov.

(Figures 3–18)

Provanna n. sp. Goedert & Campbell, 1995, figs. 4–7.

Diagnosis: A species of *Provanna* with highly variable sculpture ranging from nearly smooth to moderately cancellate. Whorls with a tabulate shoulder delineated by a spiral rib that is sometimes noded.

Explanation of Figures 3 to 18

All specimens coated with ammonium chloride. Unless otherwise indicated figures are approximately $\times 9$ and from LACMIP loc. 16504, upper part of the Lincoln Creek Formation, Canyon River, Washington.

Figures 3–18. *Provanna antiqua* Squires, sp. nov. Figures 3, 4. Paratype LACMIP 12300. Figure 3. Apertural view. Figure 4. Back view. Figure 5. Paratype LACMIP 12301, back view. Figures 6, 7. Paratype LACMIP 12302. Figure 6. Apertural view. Figure 7. Back view. Figure 8. Paratype LACMIP 12303, back

view, $\times 8.3$. Figure 9. Paratype LACMIP 12304, back view showing mineral coatings, $\times 11$. Figures 10, 11. Holotype LACMIP 12299. Figure 10. Back view. Figure 11. Right view. Figures 12, 13. Paratype LACMIP 12305. Figure 12. Apertural view. Figure 13. Back view. Figure 14. Paratype LACMIP 12306, apertural view. Figure 15. Paratype LACMIP 12307, back view. Figure 16. Paratype LACMIP 12308, back view. Figure 17. Paratype LACMIP 12309, right view, $\times 9.6$. Figure 18. Paratype LACMIP 12315 from LACMIP loc. 15911, lower Makah Formation at Shipwreck Point, back view, $\times 8.3$.



3



4



5



6



7



8



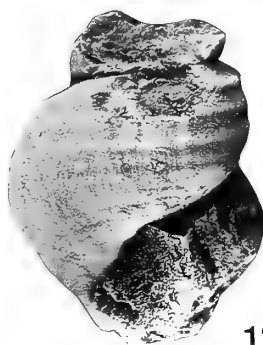
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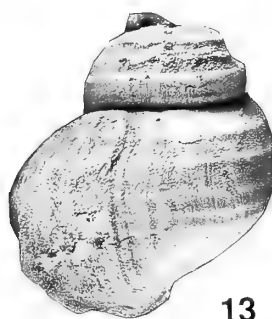
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11



12



13



14



15



16



17



18

Table 1

Measurements (mm) of *Provanna antiqua* Squires, sp. nov.

LACMIP catalog no.	H	W
12299	5.6	4.2
12300	5.4	3.9
12301	5.3	3.7
12302	5.8	4.1
12303	5.7	4.2
12304	4.5	3.3
12305	5.1	4.2
12306	5.4	4.6*
12307	5.1	4.2
12308	5.4	4.0
12309	5.3	3.7
12315	5.7	4.5

H = height; W = width. * = crushed.

Description: Shell small, up to 6 mm high, ovate fusiform. Spire elevated, approximately one-third of height of shell. Suture distinct. Body whorl moderately globose with distinct neck having one or more spiral ribs (usually weak). Whorls usually with a tabulate shoulder delineated by a spiral rib that can be noded. Whorls vary from nearly smooth (with only very weak spiral ribs or very weak axial riblets formed by rugose growth lines), to moderately sculptured (with several spiral ribs, widely but evenly spaced) to moderately cancellate (with small nodes at intersections of weak axial riblets and the stronger spiral ribs). Spiral ribs on penultimate whorl vary from zero to four; spiral ribs on body whorl vary from two (one on the shoulder and one on the neck) to approximately seven, with increasing strength toward the base. Axial riblets vary from zero to approximately 19, with minute nodes especially prominent on tabulate shoulder. Axial riblets only on posterior half of body whorl.

Holotype: LACMIP 12299.

Type locality: LACMIP 16504, upper part of the Lincoln Creek Formation, latitude 47°16'42"N, longitude 123°31'19"W.

Paratypes: LACMIP 12300 to 12309, all from LACMIP loc. 16504; and LACMIP 12315 from LACMIP loc. 15911.

Dimensions: See Table 1.

Discussion: A total of 317 specimens of the new species were found. None has the protoconch preserved. These specimens have two or three teleoconch whorls and are approximately 5 to 6 mm in height. Only 182 specimens (57%) have their shell material intact. These particular specimens show a great range in morphology, with 58% entirely smooth or smoothish, 4% axially ribbed on the body whorl shoulder, 18% spirally ribbed on one or more

whorls, and 20% cancellate on one or more whorls. There is a complete gradation from one type of morphologic form to the next, and the gradation does not follow any pattern. On the holotype (Figures 10, 11) for example, the antepenultimate whorl has only the characteristic spiral rib on the shoulder and two other very faint spiral ribs far anteriorly. The penultimate whorl has five strong spiral ribs (with the one on the shoulder noded), crossed by very low axial riblets that produce a weak cancellate sculpture. The body whorl, however, is essentially smooth with only faint spiral ribs.

At the Bear River locality (LACMIP loc. 5802) and the Canyon River locality (LACMIP loc. 15604), approximately 70% of the specimens with their shell material intact are smooth or nearly smooth, and the rest have moderate to strong sculpture. At Shipwreck Point (LACMIP loc. 15911), just the opposite was found. There, approximately 75% of the specimens with their shell material intact have moderate to strong sculpture, and the rest are smooth or nearly smooth.

A few specimens of the new species were found coated with calcareous deposits. An example is shown in Figure 9.

When compared to the other species of *Provanna*, the considerable morphologic variability of the shell of *P. antiqua* is most like *P. variabilis* Warén & Bouchet (1986: 163–164, figs. 10, 11, 13–15), a living species from the Juan de Fuca Ridge off the coast of Washington. *Provanna variabilis*, much like the new species, varies from nearly smooth (with only a few spiral ribs) to strongly spirally ribbed to cancellate, and there can be almost as much variation of the sculpture along the spire of a single specimen as in the whole material. The new species differs by having tabulate whorls, more axial and spiral ribs, and much more closely spaced ribbing.

According to Warén & Bouchet (1993), *Provanna* is usually represented by one or two species at each chemosynthetic biotope, but few of them have been recorded from more than one site. The presence of *Provanna antiqua* at four localities that are geographically and stratigraphically distinct is especially noteworthy. Warén & Bouchet (1993) also mentioned that modern species of *Provanna* are commonly highly variable in shell morphology. This is certainly true for *Provanna antiqua*. If a large number of specimens of *Provanna antiqua* had not been collected, the wide variation in morphology within this species would undoubtedly be misinterpreted, and two or more species would be "recognized."

Etymology: The specific name is derived from *antiquus*, Latin, meaning old or ancient.

Occurrence: Late Eocene and early Oligocene, western Washington. LATE EOCENE: Strata temporally equivalent to the lower part of the Lincoln Creek Formation, Bear River area near mouth of Columbia River, Washington. EARLY OLIGOCENE: Makah Formation and Jansen Creek Member of the Makah Formation, north

side of Olympic Peninsula, Clallam County, Washington. EARLIEST LATE OLIGOCENE: Upper part of Lincoln Creek Formation, Canyon River, Grays Harbor County, Washington.

ACKNOWLEDGMENTS

James L. Goedert (Gig Harbor, Washington) kindly made the specimens of *Provanna* available for study. It was his collecting with the considerable help of Gail H. Goedert and Keith L. Kaler (Olympia, Washington) that made this study possible. In addition to reviewing early versions of the manuscript, J. L. Goedert provided an important reference and various drafts of his co-authored paper on the chemosynthetic community from the Makah Formation. James H. McLean (Natural History Museum of Los Angeles County, Malacology Section) kindly helped with the identification and provided important references.

Some specimens used for this report were collected during fieldwork supported by a grant (4439-90) from the National Geographic Society to the Natural History Museum of Los Angeles County Foundation for fossil cetacean research on the Olympic Peninsula.

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- LACMIP 6958. Approximately 1 km SE of mouth of Bullman Creek, on beach terrace W½ of SW¼ of sec. 21, T. 33 N, R. 14 W, Cape Flattery U.S. Geological Survey quadrangle, 15-minute, 1957, Clallam County, Washington. Jansen Creek Member of the Makah Formation. Age: Early Oligocene. Collectors: W. Buchanan & J. L. Goedert, 1984 to date.
- LACMIP 15911. Limestone block within thin-bedded sandstone and siltstone deposits, accessible only at low tide, at Shipwreck Point, latitude 48°19'N, longitude 124°26'45"W, SE¼ of NE¼ of sec. 36, T. 33 N, R. 14 W, Sekiu River U.S. Geological Survey quadrangle, 7.5-minute, provisional edition 1984, Clallam County, Washington. About 30 m stratigraphically above top of Jansen Creek Member of the Makah Formation. Age: Early Oligocene. Collector: J. L. Goedert, 1991, 1992.
- LACMIP 16504. At elevation of 390 ft., limestone block within siltstone on the north side of a sharp bend in Canyon River, latitude 47°16'42"N, longitude 123°31'19"W, 600 m N and 290 m E of SW corner of sec. 25, T. 21 N, R. 7 W, Grisdale U.S. Geological Survey quadrangle, 7.5-minute, 1990 provisional edition, Grays Harbor County, Washington. Upper part of the Lincoln Creek Formation. Age: Earliest late Oli-

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Drilling by Buccinid Gastropods of the Genus *Cominella* in Australia

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Abstract. In laboratory experiments, two buccinid gastropods, *Cominella eburnea* (Reeve, 1846) and *Cominella tasmanica* (Tenison Woods, 1876), abundant in lagoonal sediments in southwest Australia, exhibited identical ability to prey upon soft-sediment bivalves. Both buccinids killed and consumed live, apparently healthy, small 0-year-class *Katelysia scalarina* (Lamarck, 1818) (< 1.8 cm in shell length), occasionally leaving behind drilled valves of this venerid. This represents the first record of shell drilling by a buccinid gastropod. Larger *K. scalarina* (3.1–3.8 cm) and large *Katelysia rhytiphora* Lamy, 1937 (3.9–4.6 cm) were not killed, even when their shells had chips along the margin. A third carnivorous gastropod, the muricid *Bedevea paivae* (Crosse, 1864), drilled and consumed *Katelysia* spp. in all three size-classes offered, but showed a preference for smaller individuals. Drill holes created by *B. paivae* on small *K. scalarina* could not be distinguished in shape or location from those left by the two buccinids. Consequently, these two members of the Buccinidae, along with *B. paivae*, probably contribute to the relatively intense rate of drilling mortality experienced by newly recruited *Katelysia* spp. in the lagoons of southwest Australia, but the results of these experiments do not confirm earlier suggestions that these two *Cominella* species kill larger bivalves.

INTRODUCTION

Members of the gastropod family Buccinidae, like busynine whelks in the family Melongenidae, represent a common challenge to ecologists worldwide: many species practice direct predation on live invertebrate (particularly bivalve) prey; scavenging on dead or moribund animals is also common (e.g., Dakin, 1912; Paine, 1962; Nielsen, 1975; Taylor, 1978; Kent, 1983; Himmelman, 1988; Morton & Britton, 1991). Furthermore, predatory buccinids whose feeding ecology is described in this literature are typically larger than their bivalve prey and gain access to the flesh by wedging open the valves of the prey or sometimes by chipping the margins of their shells. Consequently, detecting their ecological role is more difficult than for muricids and naticids, which drill characteristic holes in

shells of their victims (Carriker, 1981). Because gastropods are abundant and important in many assemblages of intertidal invertebrates (e.g., Roberts & Wells, 1980; Wells & Roberts, 1980), further information on their trophic relationships is necessary to understand and interpret both patterns of population fluctuations and also community dynamics in marine benthic systems (e.g., Black & Peterson, 1988; Peterson & Black, 1993).

Here we report on laboratory feeding experiments on three gastropods, including two buccinids, *Cominella eburnea* (Reeve, 1844) and *Cominella tasmanica* (Tenison Woods, 1876) and the muricid *Bedevea paivae* (Crosse, 1864), designed to assess their potential for direct predation on two soft-bottom, venerid bivalves of the genus *Katelysia*. Morton & Britton (1991) demonstrated that *C. eburnea* is attracted to and will consume disabled *Katelysia* spp. Our

study extends those results to address the question of whether, and under what conditions, any of these gastropods can successfully attack healthy, live *Katelsysia* spp.

A laboratory experiment was designed to test whether any of three common and relatively large (2–3 cm in shell length) gastropods from the sandflats of Princess Royal Harbour (Western Australia) has the capability of preying upon healthy, live *Katelsysia scalarina* (Lamarck, 1818) or *Katelsysia rhytiphora* Lamy, 1937 and, if so, whether that predation is affected by size or condition of the bivalve's shell. The gastropod consumers of most interest were the buccinids *Cominella eburnea* (Reeve, 1846) and *Cominella tasmanica* (Tenison Woods, 1876), but the muricid *Bedevea paivae* (Crosse, 1864) was also tested. Muricids are known predators on live bivalves, leaving cylindrical drill holes in their victims (Carriker & Yochelson, 1968; Vermeij, 1980; Carriker, 1981), so use of *B. paivae* served, in part, as a control to confirm that gastropod predation could take place under laboratory conditions. Furthermore, we wished to compare the relative vulnerability of individual venerid prey of differing size and shell condition to mortality from these three gastropods and to assess whether shell damage done to prey differs among the three gastropods.

MATERIALS AND METHODS

On 7 January 1984, the gastropods and bivalves needed for the experiment were collected from a sandflat in Princess Royal Harbour (35°04'S; 117°55'E) on the Southern Ocean coast of Western Australia near Albany. Experimental animals were kept in buckets of seawater for 6 hr during transport to a flowing seawater system at the Western Australian Marine Research Laboratories at Waterman. No aeration was required to keep the mollusks alive under salinity of about 35 ppt and a water temperature of about 23–25°C.

Immediately upon arrival at the laboratory, experiments were established in the flow-through seawater system. Four identical (39 × 29 × 15 cm) plastic aquaria were used. The aquaria contained no sediments, so as to maximize contact between potential predators and prey. One aquarium served as a control, whereas another received 36 *Bedevea paivae*, another 36 *Cominella eburnea*, and another 36 *C. tasmanica*. All gastropods were large (2.5–3.0 cm in shell length) adults. Into each aquarium we also placed

six replicate individuals for each of five bivalve prey categories, varying species, size, and shell condition. Specifically, each aquarium received 12 large (3.1–3.8 cm in length) *Katelsysia scalarina*, and 12 large (3.9–4.6 cm) *K. rhytiphora*, half of which for each species had naturally chipped shell margins, and six 0-year-class *K. scalarina* (< 1.8 cm). All large *Katelsysia* spp. were taken from a field experiment (Peterson & Black, 1988, 1993), for which each had been marked with dots of Mark-TeX paints; these marks indicated unambiguously which individuals began the laboratory experiment with chipped shells. Living individuals of both species of *Katelsysia* frequently possess shell damage in the form of small chips along the posterior and ventral margin (for example, 78 of 116 *K. rhytiphora* and 17 of 126 *K. scalarina* collected "wild" on 6 January 1984). These chips are illustrated by Morton & Britton (1991).

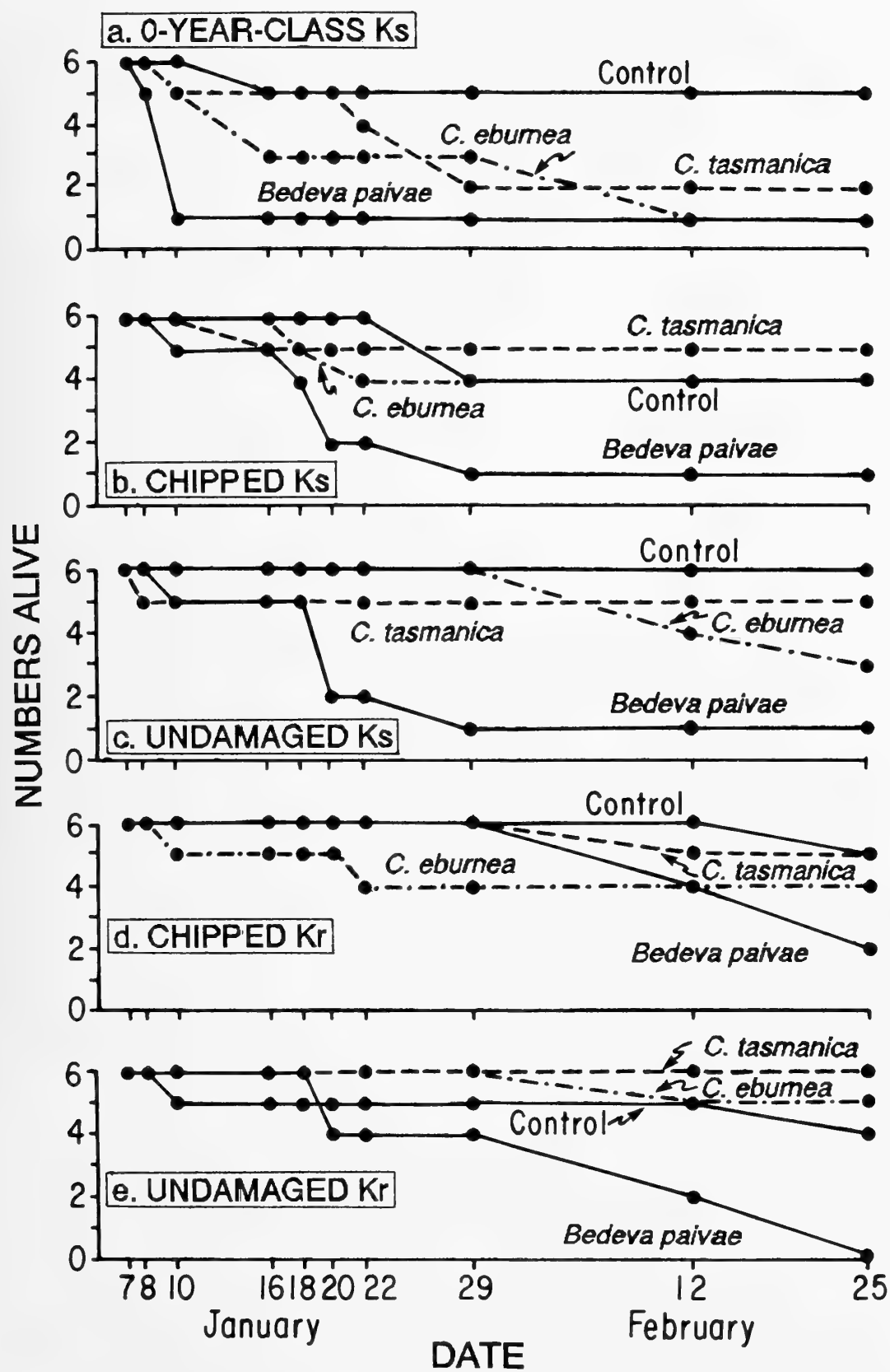
Each of the four aquaria was treated identically during the experiment with equal flow rates maintained through frequent checks. Flow was sufficient to replace the volume of each aquarium about every 15–30 min. Salinity was about 35 ppt and water temperature about 25°C. The bivalves were fed periodically (13, 18, 20, 23 January and 2 February) by shutting off the flowing seawater and adding 500–1000 ml of the cultured flagellate Tahitian *Isochrysis* at 8 million cells mL⁻¹. After 120 min, water flow was resumed. On nine occasions over a period of 50 days, all individual bivalves were inspected. Bivalve deaths were recorded separately by aquarium (equivalent to potential predator treatment) and by prey type (small 0-year-class *K. scalarina*, large chipped *K. scalarina*, large undamaged *K. scalarina*, large chipped *K. rhytiphora*, and large undamaged *K. rhytiphora*) within each aquarium. Empty shells were removed without replacement and carefully inspected for damage. None of the gastropods died during the experiment.

RESULTS

After 49 days, six of the 30 bivalves (20%) kept without gastropods had died, while 40 of 90 bivalves (44%) died in the presence of gastropods (Figure 1). This in itself suggests an effect of the gastropods, but the added presence of drilled holes in many of the dead bivalves provided direct evidence of predation. Drilling was particularly evident

Figure 1

Numbers of surviving *Katelsysia* spp. (*scalarina* = Ks; *rhytiphora* = Kr) on each of 10 dates beginning with the 7 January 1984 initiation of a laboratory assay of survivorship of bivalves of five types (0-year-class *K. scalarina* [0.6–1.7 cm]; large [3.1–3.8 cm] *K. scalarina* with chipped shell margins and without damage; and large [3.9–4.6 cm] *K. rhytiphora* with chipped shell margins and without damage) under four different carnivorous gastropod treatments (controls without consumers; 36 *Bedevea paivae*; 36 *Cominella eburnea*; 36 *Cominella tasmanica*). All gastropods had shell lengths of 2.5–3 cm. At the start of the experiment, the numbers of each of the five types of bivalve prey (a–e) were set equal at six replicate individuals in each of the four aquaria (the control aquarium plus one aquarium for each of the three carnivorous gastropods).



for the small 0-year-class *Katelsysia scalarina*. Only one of the six small *K. scalarina* died in the control aquarium without gastropods, and its shell was undamaged. In contrast, all five of the dead 0-year-class *K. scalarina* retrieved from the *Bedevea paivae* aquarium were drilled with a typical muricid drill hole and, in addition, three of the five and two of the four dead 0-year-class *K. scalarina* from the *Cominella eburnea* and *C. tasmanica* aquaria, respectively, displayed drill holes. The holes drilled by the two species of *Cominella* into shells of small *K. scalarina* could not be distinguished in shape (cylindrical) or position (scattered around the posterior and ventral margins) from those made by *B. paivae*.

Mortality of large *Katelsysia* spp., independent of species or initial shell condition, was greater in the aquarium with *B. paivae* than in the other three containers (Figure 1) and all 15 of the empty shells had drilled valves. In contrast, five of the 24 large *Katelsysia* spp. in the control aquarium without consumers were found dead with no drill marks after 49 days. Because the death rates of large *Katelsysia* spp. in the aquaria with *C. eburnea* (eight of 24) and *C. tasmanica* (three of 24) were not appreciably higher than the death rate in the container without gastropods and because only one dead bivalve exhibited additional shell damage (chipping in the *C. eburnea* aquarium) during confinement with *Cominella* spp., these results do not demonstrate a clear ability of either species of *Cominella* to cause mortality in larger individuals of *Katelsysia* spp.

Survival of large *Katelsysia* spp. with naturally chipped shells was indistinguishable from survival of those that were undamaged (Figure 1: b & d vs. c & e). *B. paivae* drilled nine large *Katelsysia* spp. with chipped shells and six without shell damage. Deaths of large *Katelsysia* spp. held with *Cominella* spp. totalled six of the 24 chipped individuals and five of the 24 with intact shells. In the aquarium without gastropods, three of 12 chipped *Katelsysia* and two of 12 undamaged individuals from the large size class died during the 49 days. Results of $2 \times 2 \chi^2$ contingency tests show that survivorship of the two *Katelsysia* species pooled at the termination of the experiment did not vary significantly with shell condition within any of the four aquaria (two-tailed P ranging from 0.21 to 0.50) nor in the pooled totals from the three aquaria containing consumers ($P = 0.50$). Furthermore, for any given consumer treatment and either species of *Katelsysia*, the time course of recorded deaths was virtually identical for chipped and unchipped bivalves in the larger size class (Figure 1: b vs. c and d vs. e). Thus, the presence of shell chips did not enhance the ability of any of the three gastropods to kill large *Katelsysia*.

Figure 1 reveals one additional pattern in the predation by *B. paivae*. Predation on *Katelsysia* spp. by *B. paivae* occurred first on the smallest individuals, the 0-year-class *K. scalarina* from 0.6–1.7 cm in shell length (Figure 1a), then on the larger *K. scalarina* of 3.1–3.8 cm in shell length (Figure 1b & c), and finally on the even larger *K. rhytiphora* of 3.9–4.6 cm in shell length (Figure 1d & e).

DISCUSSION

Our laboratory experiments confirm that *Bedevea paivae* is indeed a typical predatory muricid (Carriker, 1981), leaving cylindrical drill holes in the shells of *Katelsysia* spp. that it killed and consumed. In addition, the temporal sequence of mortality of different prey treatments in the *B. paivae* aquarium (Figure 1) suggests that *B. paivae* prefers smaller sizes of these bivalve prey despite possessing the capability of drilling and consuming the larger bivalves. Similar patterns of size selectivity have been documented for other predatory gastropod-bivalve prey systems, often explicable through application of optimal foraging theory (see reviews of Hughes, 1980, 1988; Kitchell et al., 1981; Juanes, 1992). Although he did not test for size selectivity, Vermeij (1980) described predation by *Bedevea blossvillei* on an arcid bivalve in Indonesia, noting that this species of muricid can and does prey upon bivalves that are large relative to its size. That is true also of *B. paivae* in our experiments, where *B. paivae* of 2.5–3.0 cm in height drilled individual *Katelsysia scalarina* and *K. rhytiphora* up to 3.8 and 4.6 cm in length, respectively.

We were also able to confirm the conclusion of Morton & Britton (1991) that *Cominella eburnea* is a potential predator upon *Katelsysia* spp., but the details of the predation process differ. The killing and consumption of live *Katelsysia* spp. by *C. eburnea* and *C. tasmanica* in our experiments was restricted to the small 0-year-class bivalves. Furthermore, the means of predation was drilling in a fashion indistinguishable from that of muricids like *Bedevea paivae*. We were unable to demonstrate the ability of either species of *Cominella* to kill and consume larger *Katelsysia* spp. The absence of predation on these large size classes is noteworthy given that the bivalves were offered without any sediments to use as a possible refugium from predation and without any alternative foods for the *Cominella* spp. to eat. The absence of a natural sedimentary habitat in these experiments may in some way have inhibited predation by *Cominella* spp. on the larger individuals of *Katelsysia* spp., but we observed frequent contacts between *Cominella* spp. and *Katelsysia* spp. in these aquaria with no exhibits of escape behavior by the bivalves. Furthermore, under these experimental conditions, *B. paivae* successfully killed large individuals of both species of *Katelsysia* so the absence of sediments did not prevent this known predator from consuming bivalve prey. Some of the bivalves had chipped shells, which may be expected to facilitate predation by *Cominella* spp. by allowing insertion of the proboscis into the living bivalve (Morton & Britton, 1991). Yet shell damage in the form of chips on the margin did not enhance predation rate by any of the three carnivorous gastropods in our experiments. Thus, it seems likely that the *Cominella* spp. that can be found feeding on large individuals of *Katelsysia* spp. on the sediment surface in Princess Royal Harbour (Morton & Britton, 1991; and personal observations) do not represent the cause of *Katelsysia* spp. mortality but rather are consuming moribund

and dead bivalves. The field descriptions by Morton & Britton (1991) of *Cominella eburnea* inserting its proboscis between the ventral margins of large *Katelysia* spp. lack information about the condition or health of the bivalves prior to contact with the buccinids. Further study is necessary to resolve the question of whether *C. eburnea* and *C. tasmanica* have the ability to kill large bivalves.

Our experiments show that both *Cominella eburnea* and *C. tasmanica* can kill and prey upon small bivalves, even occasionally drilling their shells. This result is important for two reasons. First, this is the first demonstration, to our knowledge, of drilling by a buccinid (see Reymont 1967; Kabat, 1990). Its drilling ability seems limited to the smaller, obviously thinner shelled individuals of *Katelysia* spp. Increased shell thickness of the bivalve prey could explain the failure of *Cominella* spp. to drill the larger venerids and could provide these prey with a size refuge from *Cominella* predation (e.g., Palmer, 1988; Tull & Bohning-Gaese, 1993), but other implications of larger size (Vermeij, 1987; Labarbera, 1989) may alternatively explain this relationship. Second, the observation of drilling on small bivalves by *Cominella* spp. contributes to an increased understanding of sources of size- and age-specific mortality in the *Katelysia* genus. Black & Peterson (1988) found high densities of small (< 1 cm in shell length), empty *Katelysia* spp. valves, many drilled, when sieving the surface sediments at Princess Royal Harbour through 1 mm mesh. This evidence of high rates of mortality in recently settled bivalves contrasts with the generally high survivorship of larger *K. scalarina*, shown by Peterson & Black (1993) to approximate 90% over multiple half-year intervals. Naticids are present at Princess Royal Harbour, as evidenced by occasional egg collars, but very rare relative to *Cominella* spp. and *Bedevea paivae*: Peterson & Black (1993) reported average pooled density of the two species of *Cominella* to be 7.02 m^{-2} and *Bedevea paivae* to occur at 0.70 m^{-2} but no naticid present in 47 m^2 of sampling. *Cominella* spp. thus appears to represent a potentially significant predator, contributing to early post-settlement mortality in southwestern Australia lagoons such as Princess Royal Harbour and Oyster Harbour. Ecologists studying invertebrate population and community dynamics in these systems and others containing abundant buccinid gastropods should now give more attention to the predatory significance of buccinid gastropods.

ACKNOWLEDGMENTS

We thank A. Hatcher and S. Vink for assistance. S. Slack-Smith and F. E. Wells of the Western Australian Museum contributed helpful guidance. W. F. Ponder and G. J. Vermeij provided commentary on buccinids. W. G. Ambrose, Jr., E. A. Irlandi, B. Roth, G. J. Vermeij, and an anonymous reviewer made useful suggestions on the manuscript. The Residency Museum in Albany through V. Milne provided accommodations. Financial support came

from NSF Grants OCE 84-15696 and INT 82-11281, and an ARGS grant.

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Note added in proof:

We recently discovered an unpublished Ph.D. thesis (Larcombe, M. F. 1971. The ecology, population dynamics, and energetics of some soft shore molluscs. Ph.D. thesis, University of Auckland, New Zealand.) that describes drilling and shell chipping as two modes of predation by four species of *Cominella* preying upon bivalves and gastropods.

Judaphos, A New Genus of Buccinid Gastropod from the Neogene of Costa Rica

by

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Abstract. *Judaphos imparabilis*, a new genus and species of Buccinidae, is described and figured. All the material was collected from the lowest 200 m of the section exposed at Punta Judas, Puntarenas Province, Pacific coast of Costa Rica. It is of probable late Miocene age. The monotypic genus differs from other buccinid genera by the appressed and channelled suture, which gives the appearance of a collar.

INTRODUCTION

In March of 1988, the field party of the Panama Paleontology Project (PPP) examined a number of fossiliferous outcrops on the Pacific coast of Costa Rica. The areas visited included the western part of the Burica Peninsula, Punta Judas, the southeastern coast of the Nicoya Peninsula, and the coastal area southeast of Puntarenas. At Punta Judas (Figure 1), 40 km WNW of Quepos, a thick sequence of volcanic sandstones, volcanic conglomerates, and litharenites is exposed (Seyfried et al., 1985). The beds dip to the east, those near the base very steeply so. This section was measured and the fossiliferous horizons carefully collected. Although the fossils were only moderately well preserved, I realized already during fieldwork that some of the specimens belonged to a genus unknown to me. Detailed study of the new material resulted in the recognition of a new genus and species, the descriptions of which follow below.

The abbreviation NMB stands for Naturhistorisches Museum Basel, Switzerland; PJ for Peter Jung localities; and CJ for Coates/Jackson localities (Anthony Coates and Jeremy Jackson, both of the Smithsonian Tropical Research Institute, Panama).

DESCRIPTION

Family BUCCINIDAE Rafinesque, 1815

Genus *Judaphos* Jung, gen. nov.

Etymology: Artificial combination of the geographic name (Punta) Judas and the generic name *Phos*. Gender: masculine.

Type species: *Judaphos imparabilis* sp. nov. Late Miocene, Costa Rica.

Diagnosis: *Judaphos* can be distinguished from other buccinid genera by its appressed and channelled suture, which gives the appearance of a collar. In apical view, the suture is undulatory wherever there are axial ribs.

Description: See description of type species.

Comparisons: *Judaphos* is more slender than *Nicema* Woodring (1964:268). The type species of *Nicema*, *N. amara* Woodring (1964:268, pl. 42, figs. 14, 15) from the lower part of the Gatun Formation (late Miocene) of Panama, has a larger apical angle than *Judaphos imparabilis*, the monotype of the genus, and a much more inflated body whorl without indication of axial sculpture.

Woodring (1964:268) assigned two additional species to *Nicema*: *Struthiolaria guttifera* Grzybowski (1899:647, pl. 19, fig. 8) from the early Miocene of Peru, which had been assigned to the genus *Northia* Gray (1847:140) by Olsson (1932:170, pl. 20, figs. 3, 9); and *Cantharus (Triumphis) predistortus* Marks (1951:117, pl. 7, figs. 8, 10, 11) from the late Miocene Daule Formation of Ecuador.

On the other hand, Olsson (1964:160) treated *Nicema* as a subgenus of *Northia* Gray, 1847, and Keen (1971:571) treated it as a subgenus of *Triumphis* Gray (1856:41). Species of *Northia*, however, are considerably more slender than species of *Nicema* or *Triumphis*. If *Nicema* is to be treated as a subgenus at all, it should go under *Triumphis* rather than *Northia*. *Judaphos*, however, clearly differs from *Triumphis* and *Nicema* by its channelled and appressed suture and by its more slender general shape.

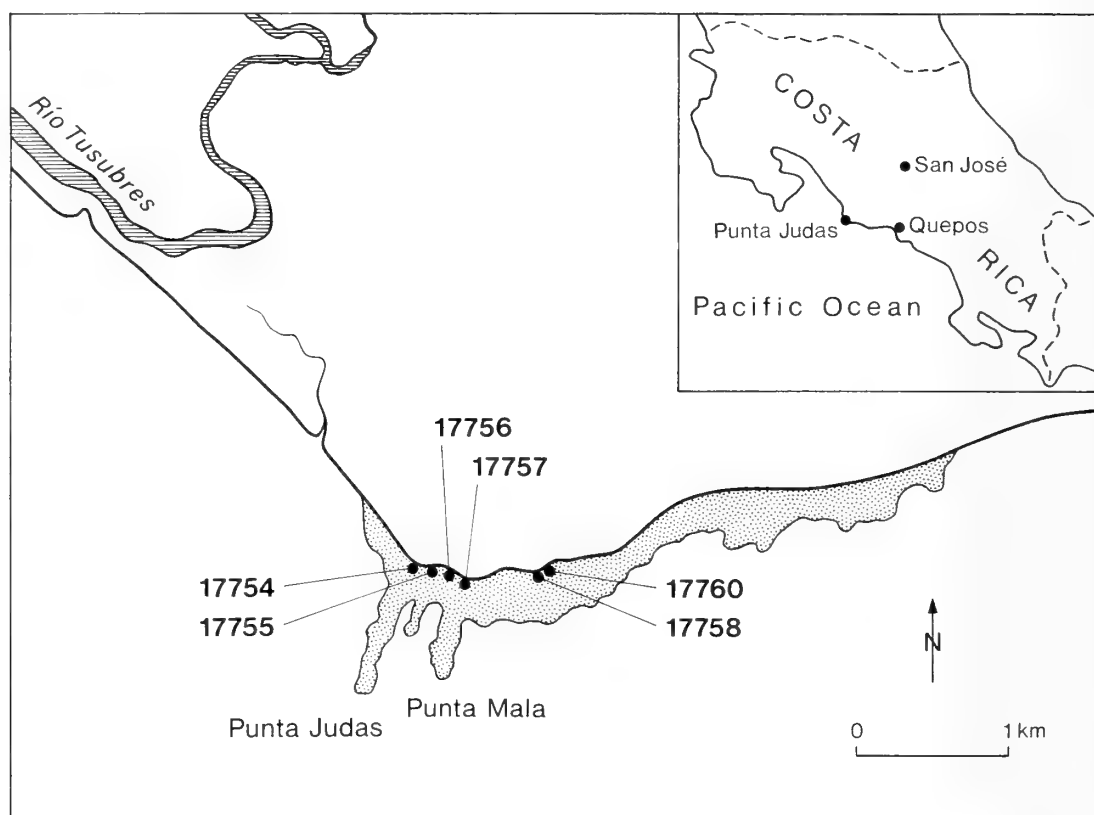


Figure 1

Map of Punta Judas and vicinity, Puntarenas Province, Costa Rica, showing location of NMB fossil localities. NMB locality 17757 is the type locality of *Judaphos imparabilis* Jung, gen. & sp. nov. The stippled area is exposed at low tide but not at high tide.

Judaphos imparabilis Jung, sp. nov.

Figures 2–7

Etymology: Latin *imparabilis* = hard to get.

Description: Shell moderately large (height ranging from 40 to 55 mm), not strongly inflated. Protoconch not known. Number of teleoconch whorls about six. First three or four teleoconch whorls sculptured by broad axial ribs that narrow somewhat adapically. Axial ribs crossed by three to four narrow spiral threads. Number of axial ribs eight to 10 per whorl. On late teleoconch whorls axial ribs inconspicuous or absent, but spiral threads covering entire body whorl. Growth lines moderately prominent, orthocline in abapical part, slightly prosocline adapically. Suture strongly

appressed, thus becoming channelled and undulatory due to axial ribs. Whorls concave in profile below suture, not shouldered. Aperture moderately wide. Columella and parietal wall covered by thin callus. Posterior canal inconspicuous, bordered by narrow ridge. Outer lip thickened, its inner surface with about 10 inconspicuous narrow lirae. Anterior canal short. Siphonal fasciole not or only slightly swollen.

Holotype: NMB H 17465 (Figures 2–5).

Dimensions of holotype: Height 48.2 mm; width 26.5 mm.

Type locality: NMB locality 17757: at high tide level behind Punta Mala, Punta Judas, 40 km WNW of Que-

Figures 2–7

Judaphos imparabilis Jung, gen. & sp. nov. 2–5. Holotype, NMB H 17465; 2: front view; 3: rear view; 4: from right side; 5: apical view. 6–7. Paratype, NMB H 17466; 6: slightly oblique front view; 7: from right side. All figures $\times 2$.



2



3



4



6



5



7

Table 1

Dimensions of selected type specimens of *Judaphos imparabilis* Jung gen. & sp. nov.

Specimen	Restored height	Restored width	H/W
NMB H 17465: holotype (Figures 2-5)	49.0	26.5	1.85
NMB H 17466: paratype (Figures 6, 7)	51.6	27.5	1.88
NMB H 17526: paratype from NMB locality 17754	55.6	28.0	1.98
NMB H 17527: paratype from NMB locality 17755	46.5	25.2	1.84
NMB H 17528: paratype from NMB locality 17756	43.6	23.0	1.89
NMB H 17529: paratype from NMB locality 17757	41.6	24.9	1.67

pos, Puntarenas Province, Costa Rica (Figure 1). Age: probably late Miocene. Costa Rican grid reference: 404/670, 385/500.

Remarks: *Judaphos imparabilis* is the type and sole species of this new genus. Only a few of the available specimens are well preserved and most are eroded or incomplete. The protoconch is missing on all specimens.

The age of the beds carrying *J. imparabilis* is not well established. Seyfried et al. (1985) considered the entire section at Punta Judas to be of middle Miocene age. Jung (1989:54), in his discussion of *Strombina colinensis* H. K. Hodson (in Hodson & Hodson, 1931), also called it middle Miocene, although all other records of *S. colinensis* are of late Miocene and early Pliocene age. Microfossil samples taken at many localities failed to yield any age-diagnostic Foraminifera. The available mollusks from the Punta Judas section suggest a late Miocene age, but they need further study before a firmer statement can be made.

Material: Six lots comprising only 14 specimens, all from the lowest part of the Punta Judas section (Figure 1).

- 1 specimen, NMB locality 17754 (= PJ 1849 = CJ-88-14-1).
- 1 specimen, NMB locality 17755 (= PJ 1850).
- 6 specimens, NMB locality 17756 (= PJ 1851).
- 3 specimens, NMB locality 17757 (=PJ 1852 = CJ-88-14-2).
- 1 specimen, NMB locality 17758 (= PJ 1853 = CJ-88-14-4).
- 2 specimens, NMB locality 17760 (= PJ 1855).

Measurements (in mm): The measurements of only six specimens are given in Table 1. The remaining eight specimens are too incomplete to be measured.

Occurrence: Lowest 200 m of Punta Judas section (late Miocene) at Punta Judas and Punta Mala, Puntarenas Province, Costa Rica (Seyfried et al., 1985:11, fig. 2).

ACKNOWLEDGMENTS

I am grateful to the Kugler-Werdenberg Foundation, Basel, for covering travel expenses, and to the Smithsonian Tropical Research Institute (STRI), Panama, for provid-

ing facilities during fieldwork. The photographs were taken by Severino Dahint of the Naturhistorisches Museum Basel, who is gratefully acknowledged. Thanks are also due to the two reviewers.

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An Extant Species of *Leptochiton*
(Mollusca: Polyplacophora) in Eocene and
Oligocene Cold-Seep Limestones,
Olympic Peninsula, Washington

by

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Abstract. Fossils of the chiton, *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846), are present in three localized cold-seep limestones on the Olympic Peninsula, Washington. One limestone is in the upper middle to upper Eocene Humptulips Formation near Humptulips; the second is in the lower Oligocene part of the Makah Formation at Shipwreck Point; and the third is in the lower upper Oligocene part of the Lincoln Creek Formation at Canyon River. The deep-sea limestones at the three localities contain dense concentrations of megabenthos that lived in association with subduction-related cold-methane seeps. Most of the chiton remains are disarticulated intermediate plates, but a well-preserved, fully articulated specimen that shows the dorsal surface was found at the Canyon River locality.

Leptochiton (*L.*) *alveolus* was previously known only as a living species with cosmopolitan distribution in deep waters. The presence of this species in the Eocene and Oligocene of Washington represents the earliest unquestionable record of this genus and the first report of an identified species of chiton from ancient cold-seeps.

INTRODUCTION

Chitons require hard substrate and commonly find it on wave-swept rocky coasts, a habitat poorly represented in the pre-Pleistocene rock record. Moreover, chitons from this high-energy environment seldom survive taphonomic processes intact. Chitons can live in deep water, and some 20 modern species are known to be endemic in depths between 200 and 6000 m (Ferreira, 1980). There is little

information available on the types of substrate that deep-water chitons prefer, but most probably live on rocks. Wu & Okutani (1984) reported deep-sea chitons living on fragments of pumice probably exposed on a muddy floor. Wolff (1979) and Sirenko (1988) reported that a few species of modern deep-water chitons live on sunken fragments of wood. Saito & Okutani (1990) reported two species of chitons living attached to rocks at a deep-sea hydrothermal vent site in the Okinawa Trough and Kulm & Suess (1990)

found chitons living on carbonate edifices, less than 1 m high, that formed around modern cold-seeps on uplifted submarine banks along the outer continental shelf-upper slope of Oregon.

Although the preservation potential for deep-water chitons seems to be good, reports of these chitons in the rock record are very rare. Only recently, Goedert & Campbell (1995) reported the first fossil chiton found associated with a deep-water, cold-seep limestone. This localized limestone is in the lower Oligocene part of the Makah Formation at Shipwreck Point, northern Olympic Peninsula, Washington. Recent collecting in other deep-water, Eocene and Oligocene rocks in Washington has yielded two additional localized, cold-seep limestone localities for this same chiton species. At all three localities, specimens of the chiton are associated with dense accumulations of worm tubes and bivalves that lived around subduction-zone related cold-methane seeps on the ocean floor. Evidently, the worm tubes and/or bivalves provided the necessary hard substrate for the chitons. At two of the localities, only disarticulated valves of the chiton were found, but at one locality, articulated specimens were found. One of these articulated specimens is remarkable because it shows the dorsal surface of all eight valves. Burial had to have been very rapid. It is the purpose of this paper to report that this chiton is the extant *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846). Goedert & Campbell (1995) identified this chiton as *Leptochiton* (?) sp.

The long geologic range of *L. (L.) alveolus* from Eocene to Recent should not be considered unusual. For example, the eastern Pacific, extant naticid gastropods *Neverita* (*Glossaulax*) *reclusiana* (Deshayes, 1839) and *Sinum scopulosum* (Conrad, 1849) have geologic records that extend back to the middle Eocene and early Oligocene, respectively (Marincovich, 1977). In addition, the eastern Pacific, extant thracioid bivalve *Thracia* (*Cetothrax*) *condoni* Dall, 1909, and the extant thyasirid bivalve *Conchocele disjuncta* Gabb, 1866, have geologic records that extend back to the Oligocene (Coan, 1990; Bernard, 1983).

Abbreviations used for catalog and/or locality numbers are: LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; LACM, Natural History Museum of Los Angeles County, Malacology Section.

STRATIGRAPHIC DISTRIBUTION AND GEOLOGIC AGES

Fragments of two valves of *Leptochiton* (*L.*) *alveolus* were found at LACMIP loc. 12385 in a localized limestone in the Humpulips Formation on the East Fork of the Humpulips River, southern Olympic Peninsula, Washington (Figure 1). The limestone was deposited in a subduction zone where subsurface methane-rich waters discharged onto the ocean floor (Goedert & Squires, 1990). The limestone is 15 m thick, 30 m long, and 15 m wide. It is highly

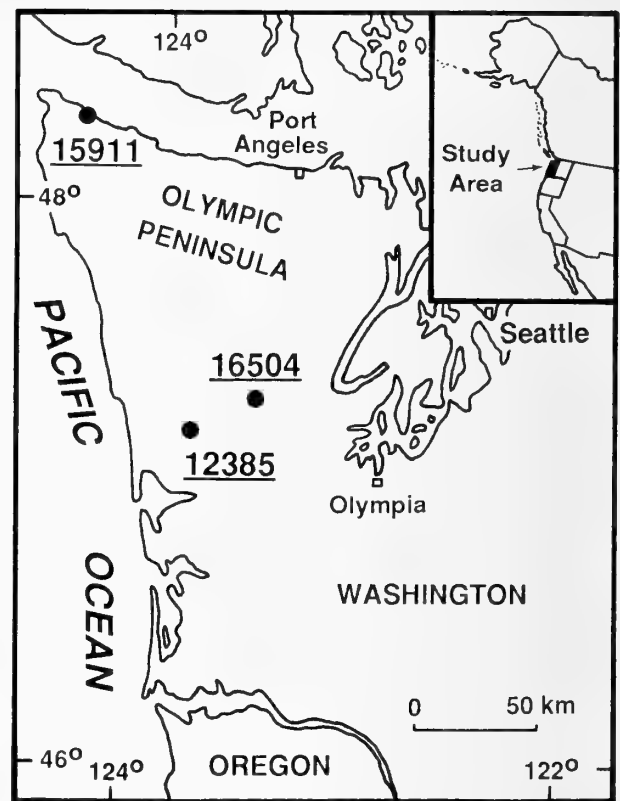


Figure 1

Index map to localities of fossil *Leptochiton* (*L.*) *alveolus*.

fossiliferous with dense concentrations of vestimentiferan? and serpulid worm tubes and numerous articulated specimens of the bivalves *Thyasira* (*Conchocele*) *folgeri* Wagner & Schilling, 1923, and *Modiolus* (*Modiolus*) *willapaensis* Squires & Goedert, 1991. Additional fossils are fissurellid?, patelliform, turbinid?, and naticid gastropods; other bivalves; a scaphopod; and decapod parts. The thyasirids and turbinids show growth series, and some of the vestimentiferan? worm tubes are vertically oriented (Goedert & Squires, 1990). Rau (1986) reported the age of the Humpulips Formation to range through much of the middle Eocene and into the late Eocene age. The exact age of the rocks at LACMIP loc. 12385 is not known, and until calcareous nannofossil studies are made on the surrounding siltstone, only a broad age range of late middle Eocene to late Eocene can be assigned (Goedert & Squires, 1990; Squires & Goedert, 1991) (Figure 2).

Two articulated specimens, as well as seven separate valves and two clusters of several valves, of *Leptochiton* (*L.*) *alveolus* were found at LACMIP loc. 16504 in a small limestone block in the upper part of the Lincoln Creek Formation at Canyon River, in the Satsop River area, southern Olympic Peninsula, Washington (Figure 1). Prothero & Armentrout (1985) reported that the Lincoln Creek Formation in the Canyon River area is late Eocene

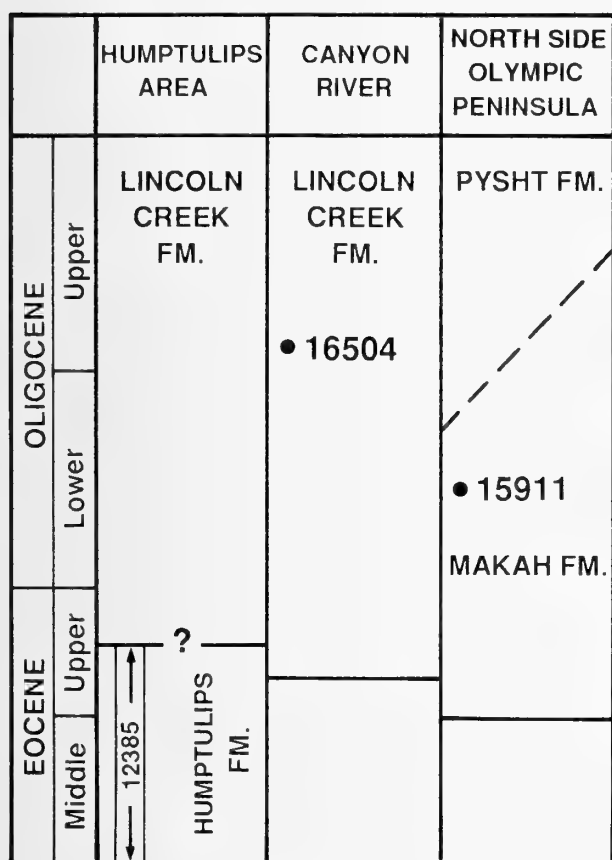


Figure 2

Chronostratigraphic chart showing position of localities for fossil *Leptochiton* (*L.*) *alveolus*.

to late Oligocene in age. The limestone at LACMIP loc. 16504 is a cold-methane-seep deposit containing a diverse chemosynthetic community with numerous specimens of the gastropod *Provanna antiqua* Squires, 1995. The rocks at the locality are earliest late Oligocene in age (Squires, 1995) (Figure 2). The details of the petrology and taxonomic composition of the limestone are under study by the junior author and K. L. Kaler.

Twenty separate valves of *Leptochiton* (*L.*) *alveolus* have been found at LACMIP loc. 15911 in a one-meter-thick limestone block in the Makah Formation at Shipwreck Point, northern Olympic Peninsula, Washington (Figure 1). Snively et al. (1980) reported that the Makah Formation is late Eocene to late Oligocene in age. Most of the *Leptochiton* specimens were found during the study by Goedert & Campbell (1995) of the paleoenvironment of the limestone. The limestone is a cold-methane-seep deposit containing abundant specimens of the bivalves *Modiolus* (*M.*) *willapaensis* and *Calyptogena chinookensis* Squires & Goedert, 1991, in association with vestimentiferan? worm tubes, scaphopods, many archaeogastropods

and other gastropods (including *Provanna antiqua*), other bivalves, crustacean fragments, and wood fragments (Goedert & Campbell, 1995). Goedert & Campbell (1995) and Squires (1995) reported that the rocks at LACMIP loc. 15911 are early Oligocene in age.

SYSTEMATIC PALEONTOLOGY

Class Polyplachophora Gray, 1821

Order Neoloricata Bergenhayn, 1955

Suborder Lepidopleurina Thiele, 1910

Family LEPTOCHITONIDAE Dall, 1889

Genus *Leptochiton* Gray, 1847

Type species: *Chiton cinereus* Montagu, 1803 [= *Leptochiton asellus* (Gmelin, 1791)], by subsequent designation (Gray, 1847).

Discussion: There has been considerable confusion regarding whether or not *Leptochiton* should stand as a genus, be put in synonymy with *Lepidopleurus* Risso, 1826, or be made a subgenus of *Lepidopleurus*. Ferreira (1979) reviewed the nomenclatural history of *Leptochiton* and concluded that it should have full generic rank. Kaas & Van Belle (1985) also recognized *Leptochiton* as a distinct genus.

Subgenus *Leptochiton sensu stricto*

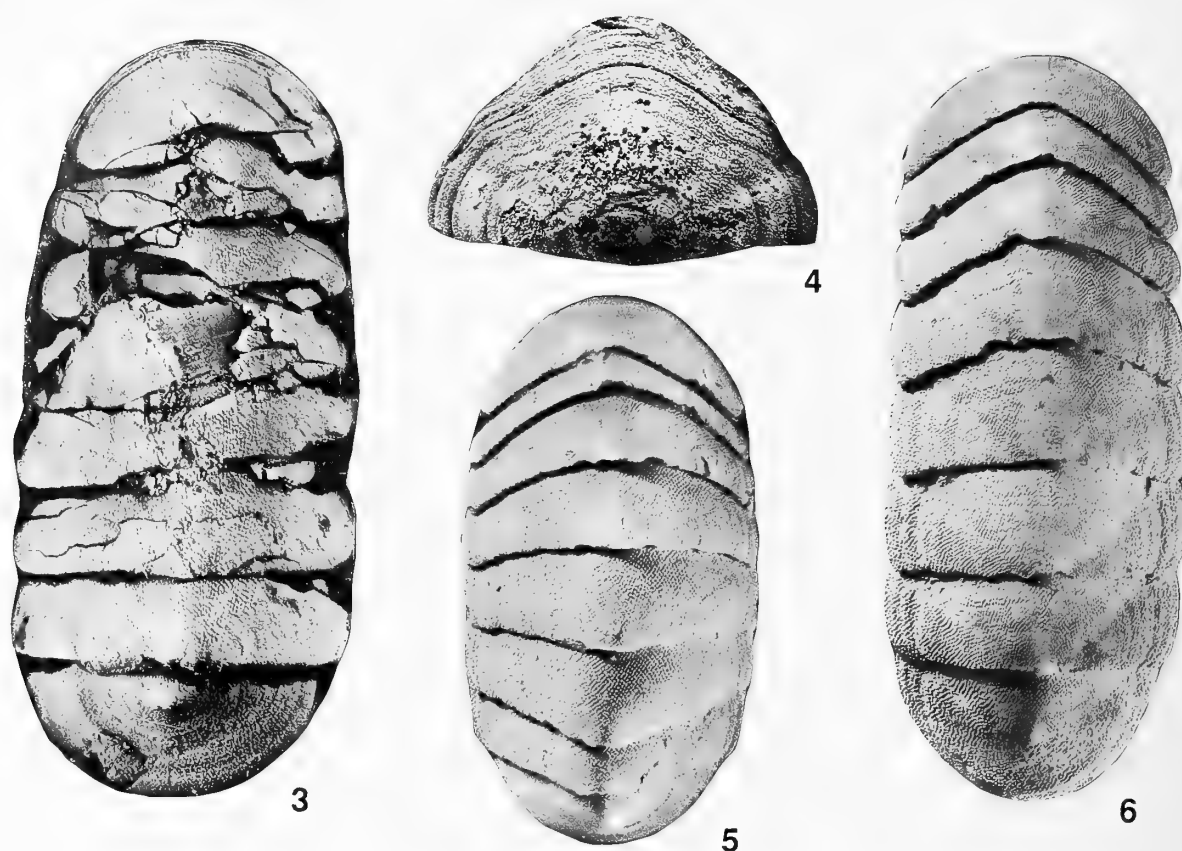
Leptochiton (*Leptochiton*) *alveolus* (Lovén, 1846)

(Figures 3–6)

Chiton alveolus M. Sars MS, Lovén, 1846:159. [For synonymies of this species, see Ferreira (1979) and Kaas & Van Belle (1985).]

Discussion: Three articulated specimens and 37 separate valves were found. The best preserved specimen (Figure 3) is extremely unusual for a fossil chiton because it is fully articulated. It shows the dorsal surface, but the ventral surface is encased in hard limestone. Chitons commonly curl up after death, but this specimen is flat and, most likely, was buried while alive. The specimen has suffered some fracturing and mild crushing, and its length seems to have been shortened slightly due to the valves having been pushed together. A second fully articulated specimen is very crushed.

The fossils from Washington were compared to every known fossil and Recent species of *Leptochiton*. The fossil species of *Leptochiton* are listed by Van Belle (1981) and the Recent species are discussed in Kass & Van Belle (1985). The fossil specimens from Washington are morphologically indistinguishable from *Leptochiton* (*L.*) *alveolus*, heretofore known only as an extant species. The Washington fossil specimens are like *L.* (*L.*) *alveolus* in the following features: arched, thin valves with convex slopes; the head valve is semicircular; the intermediate valves seem to be weakly keeled although crushing has



Explanation of Figures 3 to 6

Figures 3-6. *Leptochiton* (*Leptochiton*) *alveolus* (Lovén, 1846). Figures 3, 4. Fossil specimens. Figure 3. LACMIP 12334, LACMIP loc. 16504, upper part of the Lincoln Creek Formation at Canyon River, dorsal view, $\times 6.1$. Figure 4. LACMIP 12322, LACMIP loc. 15911, lower Oligocene Makah Formation at Shipwreck Point, dorsal view of an intermediate plate, $\times 7.4$. Figures 5, 6. Recent specimens. Figure 5. LACM 49-309.9, Bering Sea, Alaska, dorsal view showing a partially enrolled specimen, $\times 7.1$. Figure 6. LACM 66-85.1, Peru, dorsal view showing a slightly enrolled specimen, $\times 4.5$.

made this feature difficult to distinguish; and the tegmen-tum is covered with evenly disposed, minute granules whose size can vary slightly from place to place. The articulated fossil (LACMIP 12334) in Figure 3 is 16.1 mm long and 6.9 mm wide, whereas modern specimens of *L. (L.) alveolus* have been reported by Kaas & Van Belle (1985) up to 30 mm, and rarely, 40 mm long. An examination of the LACM collection of Recent specimens of *L. (L.) alveolus* from Alaska to Peru revealed the following variations in morphology: degree of elongation of the shell (length/width ratios vary from approximately 1.7 to 2.5), strength of the granules (from weak to moderately coarse), spacing of the granules (usually evenly disposed, but on some valves, the granules are coarser on the central area), strength of the lateral area (weakly defined to distinct), strength of the mucro (from low to prominent), and location of the mucro (from medially to anterior). Two Recent specimens, one from LACM lot 49-309 (Bering Sea, Alaska) and the other from LACM lot 66-85 (Peru), are shown in Figures

5 & 6, respectively. The specimen in Figure 5 is less elongate than the one in Figure 6 and has a more anteriorly located mucro. The articulated fossil of *L. (L.) alveolus* (LACMIP 12334) is moderately elongate (length/width ratio of 2.3), weakly granulate with slight variations in granule size, and has a prominent mucro very anteriorly located. It may be that the anterior position of the mucro in the fossil is due to post-burial compression although the mucro's location is within the observed range in Recent specimens.

Leptochiton (*L.*) *alveolus* was not known from the eastern Pacific until Ferreira (1979) expanded the definition of *L. (L.) alveolus* and put the eastern Pacific *L. (L.) belknapi* Dall, 1878, into synonymy with *L. (L.) alveolus*. According to Wu & Okutani (1984), and as accepted by Kaas & Van Belle (1987), there is slight but significant morphological distinction between *L. alveolus*, which they claim is restricted to the Atlantic Ocean, and *L. belknapi*, which they claim is confined to the Pacific and Indian Oceans. We

examined five lots of eastern Pacific *Leptochiton* in the LACM collection and found specimens that have features of both species. For example, we observed specimens from lot 49–309 (Bering Sea) whose anterior margin of the tail valve is almost straight (a feature of *alveolus*) and whose intermediate valves are keeled (a feature of *belknapi*). In addition, a specimen from this lot has one pair of sulci radiating from the apex (a feature of *alveolus*) on intermediate valves 4 and 7 and two pairs of these sulci (a feature of *belknapi*) on the others intermediate valves. Our observations indicate that these two species intergrade and that Ferreira (1979) was justified in regarding them as the same species.

Modern *L. (L.) alveolus* is one of the two known cosmopolitan species of chiton. Clark (1994) reported the other species to be the mopalid *Placiphorella atlantica* (Verrill & Smith, 1882). *Leptochiton (L.) alveolus* is present in the Pacific, Atlantic, and Indian Oceans, and in the Mediterranean Sea, and the latitudinal range of this species is approximately 72°N (Point Barrow, Alaska) to 50°S (Kerguelen Islands, southern Indian Ocean) (Van Belle, 1975; Ferreira, 1979; Kaas, 1981). It is rarely found in depths of less than 100 m, and its favored habitat is in bathyal to abyssal depths (as deep as 4825 m) (Ferreira, 1979; Kaas & Van Belle, 1985). There is scant information about the types of substrate that this species lives on in modern oceans. Specimens of *Leptochiton (L.) alveolus*? have been found living on manganese nodules and crusts dredged from 4500 m in the equatorial north Pacific Ocean (D. J. Eernisse, personal communication). So far *L. (L.) alveolus* has not been reported as a member of a modern chemosynthetic community, but there is a good likelihood that this species will be found based on its habitat in the past and on its modern cosmopolitan distribution in deep waters. In addition, chemosynthetic habitats commonly contain benthic invertebrates whose ancestries are long ranged (Newman, 1985).

The only living species of *Leptochiton* that has been reported from a chemosynthetic community is *L. tenuidontus* Saito & Okutani (1990), which has been found at a hydrothermal vent site at 1395 m depth in the Okinawa Trough, east China Sea. *Leptochiton tenuidontus*, which is known from only a single eroded specimen, differs from the *L. (L.) alveolus* by having the following features: wider shell, coarser granules, and more rows of transverse radial teeth.

Previously, the earliest geologic record of *Leptochiton sensu stricto* was questionable. Van Belle (1981), in his very useful catalog of fossil species of chitons, listed *Leptochiton ? deshayesi* (Terquem, 1852) from Lower rocks of Early Jurassic age in France and *Leptochiton ? fischeri* (Rochebrune, 1883) from rocks of late middle Eocene age (Bartonian Stage) in France. His only other Eocene record of this genus is *L. magnograni* (Ashby, 1925) from Muddy Creek, Victoria, southeastern Australia; however, an Eocene age for Ashby's species cannot be corroborated. Ashby (1925) reported that the horizon for *L. magnograni-*

fer is unknown. There are no Eocene rocks in the Muddy Creek area, but there are Miocene through Pleistocene rocks (Spencer-Jones, 1971). The fossil specimens of *L. (L.) alveolus* from the late middle Eocene to late Eocene Humptulips Formation in Washington, therefore, represent the earliest known record of *Leptochiton sensu stricto*.

The only other reports of Eocene chitons from the Pacific coast of North America are from the middle Eocene (molluscan "Transition Stage") basal part of the Tejon Formation, Tehachapi Mountains, southern California. Squires (1989) and Lindberg & Squires (1990) reported unidentified chiton fragments associated with abundant rocky intertidal mollusks in these rocks. The chiton fragments, which are poorly preserved, are probably referable to genus *Stenoplax* (R. N. Clark, personal communication).

All Oligocene records *Leptochiton sensu stricto*, other than those in the Makah and Lincoln Creek Formations of Washington, are in Europe (Van Belle, 1981), but none is *L. (L.) alveolus*. *Leptochiton sensu stricto* was also present in Europe during the Miocene and was present in Australia during the Miocene and Pliocene (Van Belle, 1981), but none of these species is conspecific to *L. (L.) alveolus*.

The only other fossil species of *Leptochiton* reported from the Pacific coast of North America is *L. clarki* Berry (1922: 427–430, pl. 1, fig. 10, text figs. 1–4) from the Pleistocene at Santa Monica, California. *Leptochiton clarki* differs from *L. (L.) alveolus* by having distinct rows of small granules, weak longitudinal riblets on the central area, and radial riblets laterally. Today, numerous species of *Leptochiton* live off the Pacific coast of North America (Ferreira, 1979; Kaas & Van Belle, 1985).

Lepidochitona (Spongiaradsia) lioplax (Berry, 1922: 431–433, pl. 1, figs. 1–6) from the Sooke Formation on southern Vancouver Island, British Columbia, Canada, is the only other Paleogene chiton from the Pacific coast of North America that has been named and described. Moore & Addicott (1987) reported the age of the Sooke Formation to be late Oligocene to earliest Miocene.

Distribution: Late middle Eocene to late Eocene to early late Oligocene (Washington) to Recent (cosmopolitan). LATE MIDDLE EOCENE to LATE EOCENE: Humptulips Formation, Humptulips area, southern Olympic Peninsula, Washington. EARLY OLIGOCENE: Makah Formation, northern Olympic Peninsula, Washington. EARLIEST LATE OLIGOCENE: Upper part of Lincoln Creek Formation, Canyon River, southern Olympic Peninsula, Washington. RECENT: Cosmopolitan, in the Pacific, Atlantic, and Indian Oceans, and the Mediterranean Sea.

ACKNOWLEDGMENTS

The considerable help of Keith L. Kaler (Olympia, Washington) and Gail H. Goedert in collecting the specimens made this study possible. Roger N. Clark (Klamath Falls, Oregon) helped greatly in the identification, and shared his knowledge of chitons. William A. Newman (Scripps

Institution of Oceanography, La Jolla, California) provided identification help in the early phase of this study. James H. McLean (Natural History Museum of Los Angeles County, Malacology Section) allowed access to modern specimens of *Leptochiton* and to the Malacology Section library. The manuscript benefited from critical reading and insightful comments by Douglas J. Eernisse (Laboratory of Molecular Systematics, Smithsonian Institution) and an anonymous reviewer.

Some specimens used for this report were collected during fieldwork supported by a grant (4439-90) from the National Geographic Society to the Natural History Museum of Los Angeles County Foundation for fossil cetacean research on the Olympic Peninsula.

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- LACM lot 66-85. At 3070 m depth, muddy bottom, abyssal Pacific, south of Callgo, Peru (15°34'S, 77°36'W). Anton Brunn, Cruise 17, by Agassiz Trawl. July, 1966.
- LACMIP 12385. Limestone deposit cut by an abandoned meander on the East Fork of Humptulips River, latitude 47°15'17"N, longitude 123°49'00"W, in the NW part of sec. 4, T 20 N, R. 9 W, Quinault Lake U.S. Geological Survey quadrangle, 15-minute, 1955, Grays Harbor County, southern Olympic Peninsula, Washington. Humptulips Formation. Age: late middle Eocene to late Eocene. Collector: J. L. & G. H. Goedert, 1990.
- LACMIP 15911. Limestone block within thin-bedded sandstone and siltstone deposits, accessible only at low tide, at Shipwreck Point, latitude 48°19'N, longitude 124°26'45"W, SE¼ of NE¼ of sec. 36, T 33 N, R. 14 W, Sekiu River U.S. Geological Survey quadrangle, 7.5-minute, provisional edition 1984, Clallam County, northern Olympic Peninsula, Washington. About 30 m stratigraphically above top of Jansen Creek Member of the Makah Formation. Age: early Oligocene. Collectors: J. L. & G. H. Goedert, 1991-1993.
- LACMIP 16504. At elevation of 390 ft., limestone block within siltstone on the north side of a sharp bend in Canyon River, latitude 47°16'42"N, longitude 123°31'19"W, 600 m N and 290 m E of SW corner of sec. 25, T. 21 N, R. 7 W, Grisdale U.S. Geological Survey quadrangle, 7.5-minute, 1990 provisional edition, Grays Harbor County, southern Olympic Peninsula, Washington. Upper part of the Lincoln Creek Formation. Age: earliest late Oligocene. Collectors: J. L. & G. H. Goedert, & K. L. Kaler, 1993.
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Direct Observation of Encapsulated Development in Muricid Gastropods

by

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Abstract. Although muricid gastropods produce a spectacular array of benthic egg capsules, many aspects of their encapsulated development remain poorly studied. This may be due in part to the fact that the capsule walls of many species are opaque, and attempts to rear early-stage embryos outside these structures have proved to be difficult. I describe a technique that allows developmental changes in the behavior and morphology of muricid embryos to be observed through the inner capsule wall. By selectively removing the thick and often opaque outer wall laminae of muricid egg capsules, embryos may be observed through the remaining transparent inner wall. Although embryos within stripped capsules are still vulnerable to contamination by protists and bacteria, embryos of the marine gastropod *Nucella emarginata* ("northern species") have been successfully reared in stripped capsules when cultured under sterile conditions. Hence, this technique provides a window through which to view the entire intracapsular development of muricid gastropods.

Stripped capsules may also be used to examine specific benefits and costs associated with the enclosure of embryos within benthic capsules. Because stripped capsules lack the protective outer wall laminae, embryonic development within stripped and whole capsules can be compared to assess (1) the benefits of these laminae in protecting embryos from specific sources of mortality, and (2) their costs in terms of limiting the diffusion rate of oxygen and metabolic wastes into and out of the capsule chamber. Thus, this technique also has the potential to be an invaluable tool in helping to understand the role of encapsulating structures in gastropod life histories.

INTRODUCTION

A wide variety of organisms enclose their eggs within some form of protective covering. These structures vary tremendously in form, ranging from the calcareous egg shells of many terrestrial vertebrates to the flexible, proteinaceous capsules of higher prosobranch gastropods. Because egg coverings are often thick-walled, composed of multiple laminae, and partially opaque, numerous techniques have been employed to investigate the development of embryos within these structures. Such techniques have often involved the chemical or mechanical removal of portions of egg coverings in order to observe embryonic development more clearly (e.g., avian egg shells: Tolhurst, 1974) or to determine the resistance of specific laminae to solute transport, thermal stress, and desiccation (insect egg cases: McFarlane, 1978; spider cocoons: Hieber, 1985, 1992).

Other methods have involved the physical removal of embryos from their encapsulating structures in order to manipulate embryonic development experimentally or to determine the ability of embryos to develop outside these protective confines (e.g., gastropod capsules: Clement, 1952; Perron, 1981; Pechenik et al., 1984; Lord, 1986). These techniques have not only increased our understanding of embryonic development within opaque egg coverings, but have also helped to identify the role of encapsulating structures in protecting embryos from specific sources of mortality.

Marine gastropods within the family Muricidae are typical of most higher prosobranch snails in that they enclose developing embryos within elaborate, structurally complex, benthic egg capsules. Embryos remain within these capsules for varying portions of their development before emerging as either planktonic larvae or juvenile

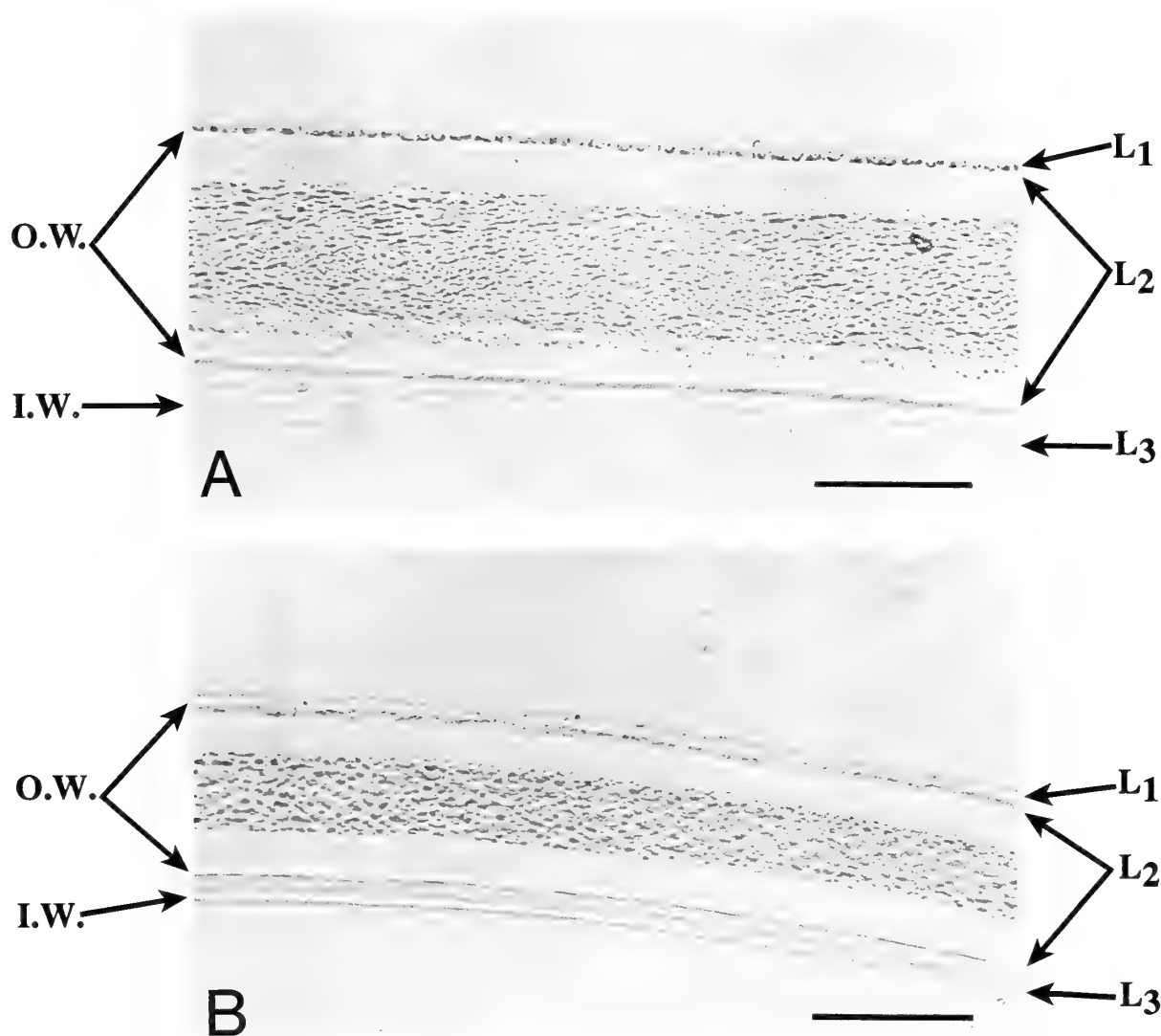


Figure 1

Light micrographs of transverse sections through the multilaminated capsule walls of two muricid snails: (A) *Nucella emarginata* and (B) *N. lamellosa*. Symbols L₁–L₃ refer to the three laminae visible in the capsule wall of these species using light microscopy. Also identified are the two major regions of the capsule wall: the outer capsule wall (O.W.) comprising laminae L₁ and L₂, and the inner capsule wall (I.W.) consisting of the innermost lamina, L₃. The opaque outer wall was the portion of the capsule removed during the stripping process. The scale bars represent 50 μ m.

snails (D'Asaro, 1991). Although numerous studies have described sequential stages in the morphogenesis of muricid embryos (e.g., D'Asaro, 1966; Gallardo, 1979; Roller & Stickle, 1988), few have documented changes in the growth and behavior of embryos during their encapsulated development. This may be because capsule walls of many species are opaque, and the few attempts to rear early-stage embryos outside these structures have proved to be difficult (Pechenik et al., 1984; Stöckmann-Bosbach, 1988; but see Lord, 1986). Also, since many encapsulated embryos are enclosed with nutritive reserves, such as nurse

eggs (Spight, 1976; Gallardo, 1979) and albumen (D'Asaro, 1966; Rivest, 1986; Stöckmann-Bosbach & Althoff, 1989), observations made on embryos cultured in an artificial fluid environment may not accurately reflect natural development within the egg capsule.

Here I describe a simple technique for removing the opaque outer capsule wall that not only enables the entire embryonic development of muricid snails to be followed within the egg capsule, but also allows embryos to remain within their natural medium. Hancock (1956) and Ganaros (1958) first indicated that the outer capsule wall of the

muricid snail *Urosalpinx cinerea* (Say, 1822) could be peeled to allow direct observation of the embryos within. To my knowledge, however, this technique has never been described, nor has it been used to follow the developmental sequence of embryos over time. The laminated nature of muricid egg capsules makes itself amenable to this type of manipulation. Egg capsules within the family Muricidae are typically composed of three to four discrete laminae (Figure 1; see also D'Asaro, 1988; Roller & Stickle, 1988): an outer protective lamina, L_1 ($\leq 5 \mu\text{m}$), which seals the whole capsule including the escape aperture; a thick middle lamina, L_2 (usually $< 100 \mu\text{m}$), which comprises the internal skeleton of the capsule wall and is often composed of multiple fibrous layers; and one or two inner laminae, L_3 , and L_4 (collectively $< 6 \mu\text{m}$; D'Asaro, 1988), often not distinct from one another at the level of light microscopy, but which act to enclose the developing embryos and intracapsular fluid within a transparent chamber. The technique described herein relies on the separation of the outer capsule wall laminae L_1 and L_2 (hereafter collectively termed the "outer capsule wall"; Figure 1) from the thinner innermost laminae L_3 and L_4 (hereafter collectively termed the "inner capsule wall"; Figure 1). Although the following tests of this method were conducted on egg capsules of the muricid snail, *Nucella emarginata* (Deshayes, 1839), this method has also been used on capsules of *Nucella lamellosa* (Gmelin, 1791; Figure 1) and *Nucella canaliculata* (Duclos, 1832), and should be applicable to other muricid capsules with a similar type of capsule wall microstructure.

MATERIALS AND METHODS

Stripping Egg Capsules of *Nucella emarginata*

Freshly laid egg capsules were collected from laboratory-raised females of the "northern species" of *Nucella emarginata* (see Palmer et al., 1990). The outside surface of each capsule was sterilized prior to removing portions of the outer capsule wall by briefly swabbing the capsule exterior with absorbent cotton soaked in 70% ethanol. Exposure to alcohol also caused capsules to dehydrate rapidly. This process aided in the separation of the outer capsule wall from the capsule chamber (see below), and did not appear to have any adverse effects on embryonic development. It should be noted, however, that the use of 70% ethanol was not essential for the successful stripping of capsules and subsequent culture of encapsulated embryos.

The outer capsule wall was stripped away from the underlying inner capsule wall using a disposable Reichert Histostat microtome blade. The initial cut into the capsule wall was made at an angle approximately 15° to the capsule surface, near the junction of the capsule chamber and plug, and at the region of the capsule seam; the capsule wall is usually slightly thickened along the length of the capsule chamber in the region of both seams. Once the initial incision was made, the buckling outer capsule wall tended

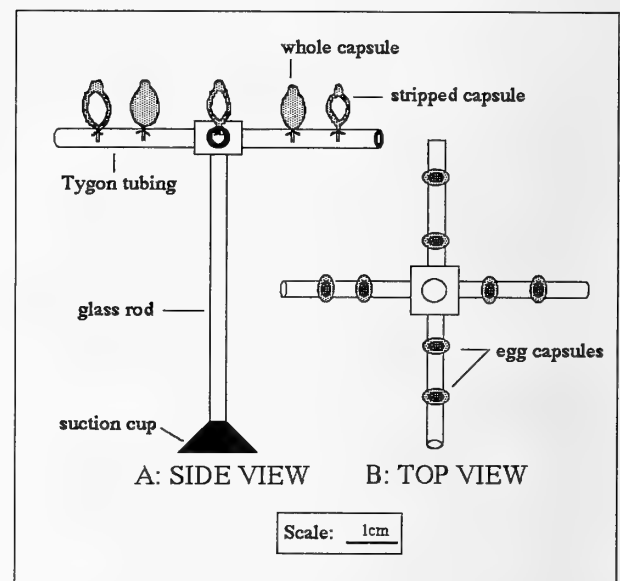


Figure 2

Side view (A) and top view (B) of stripped and whole capsules positioned within their Tygon® holders in the UV sterilized seawater treatment.

to return to its normal shape, leaving the inner wall deflated due to the evaporation of water from the chamber. As the capsule continued to lose water, the inner wall gradually peeled further away from the surface of the outer wall, thus allowing the outer wall to be removed piecemeal with little chance of rupturing the underlying chamber. Once approximately two-thirds of the outer wall had been removed on one side of the capsule, the capsule was repositioned and the process repeated on the opposite side. At the end of these procedures, two panels of approximately equal size had been removed from the outer capsule wall. Although the entire outer wall could be removed following this technique, I elected not to do this, since capsules are more easily damaged during handling without a portion of the outer wall or stalk for structural support. Once capsules were stripped, they were then placed in petri dishes of $1 \mu\text{m}$ filtered, autoclaved, antibiotic-treated seawater (0.050 g/L streptomycin; 0.030 g/L penicillin) for 1 day to determine if there were any leaks in the capsule chamber. Because the intracapsular fluid of freshly laid *Nucella* capsules is extremely viscous (Pechenik et al., 1984; Stöckmann-Bosbach & Althoff, 1989; Rawlings, personal observation), any tears in the inner capsule wall were evident from the discharge of this fluid from the capsule chamber into the surrounding seawater.

Culture Conditions

Since embryos within all stripped capsules failed to survive when cultured in $1 \mu\text{m}$ filtered flowing seawater, I attempted to minimize the exposure of capsules to bacteria

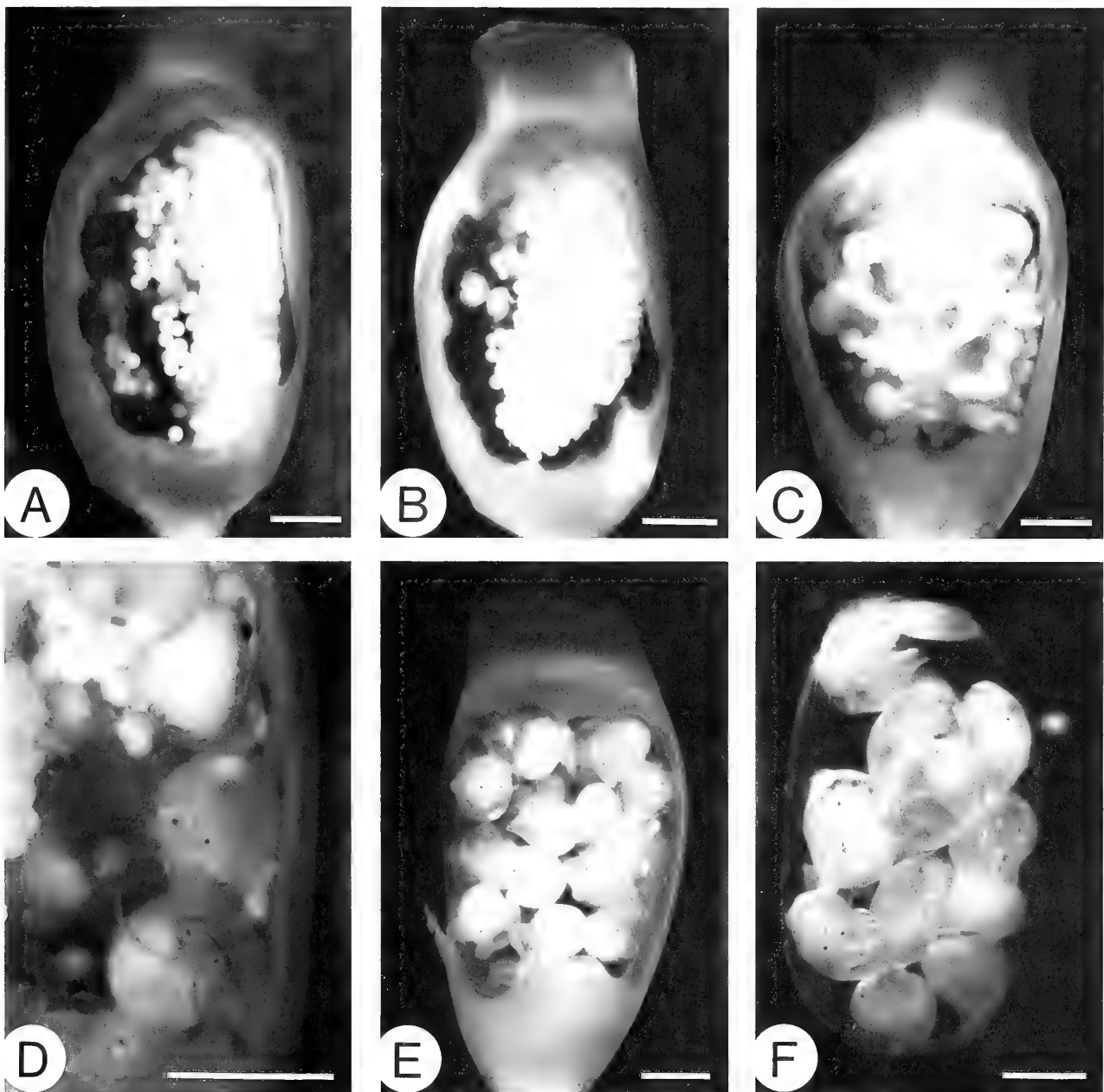


Figure 3

Developmental sequence of encapsulated embryos of *Nucella emarginata* enclosed within stripped egg capsules. Development times refer to the number of days since capsules were collected from a spawning female. Descriptions of each photographic plate are as follows. (A) Stripped capsule 7 days after collection, illustrating the viscous nature of the capsular fluid and difficulty in distinguishing between nurse eggs and developing embryos at this developmental stage. (B) The same capsule as in (A), 36 days after collection. Note the change in the consistency of the capsular fluid, suggesting the uptake of albumen during development by embryos, and the presence of ciliated late 2nd-stage/early 3rd-stage veligers (see LeBoeuf, 1971, for a description of veliger stages of *N. emarginata*). (C) Thirty-six-day-old 3rd-stage veligers readily consuming nurse eggs within the capsule chamber. This capsule was collected from the same clutch as the capsule in (A) and (B), indicating differences in development rate of embryos among capsules, possibly due in part to differences in the actual spawning date of capsules within a clutch. (D) The same capsule as in (C) at 60 days of development, illustrating early 4th-stage veligers with an excess of unconsumed nurse eggs. (E) Fourth-stage veligers at 60 days of development, revealing the close packing of embryos within the chamber and the complete consumption of all nurse eggs. (F) Newly metamorphosed juveniles within a completely stripped capsule. This capsule was stripped three days prior to the hatching of embryos from the capsule. Scale bars represent 1 mm in all photographs.

and protists by raising capsules in (a) sterile glass petri dishes containing 1 μm filtered, autoclaved, antibiotic-treated seawater, and (b) flowing, 1 μm filtered, ultraviolet (UV) sterilized seawater. For each treatment, pairs of capsules were collected from freshly deposited laboratory-laid clutches of egg capsules. One capsule from each pair was then "stripped," as previously described, and the other capsule was left intact ("whole" capsule).

In the treatment using autoclaved, antibiotic-treated seawater, each pair of capsules was assigned to one glass petri dish, and capsules were cultured in an incubator at 12°C. Glass dishes and seawater were changed at approximately 5 day intervals, at which time embryos were examined for development. Embryos were considered to have died when they turned pink, ceased to move their velar cilia, or began to disintegrate within the capsule.

In the UV sterilized seawater treatment, each pair of capsules was placed in holders made from Tygon® tubing (Figure 2). Stripped and whole capsules from the same clutch were placed side by side in Tygon® holders by inserting their stalks into small slits perpendicular to the length of the tubing. Each Tygon® holder was attached to the base of a 10 l culture chamber using a glass rod and suction cup, thus keeping capsules suspended at a height of approximately 10 cm from the bottom of the chamber. In this manner, capsules were exposed to flow rates of 2 L/min of UV sterilized water, and seawater temperatures ranging from 10–12°C. Survival of encapsulated embryos was monitored at 4–8 day intervals, at which time capsules were also gently swabbed to remove any surface debris. Capsule holders were changed at two-week intervals.

RESULTS

Embryos completed development successfully within 53% of 32 stripped capsules exposed to autoclaved, antibiotic-treated seawater, and within 40% of 58 stripped capsules exposed to UV sterilized seawater (Table 1) over development times ranging from 52 to 77 days at 10–12°C. In those capsules in which embryos successfully hatched, no significant differences were evident in the number of hatchlings emerging from paired stripped and whole capsules (Paired t-test: $t = 1.52$, $P = 0.15$; $n = 15$ pairs [UV treatment, September 1993]), with means (\pm SE) of 12.3 ± 1.80 and 10.4 ± 1.66 embryos hatching from stripped and whole capsules, respectively.

The whole course of embryonic development was observed through the transparent inner wall of stripped egg capsules (Figure 3), including such events as: the initial reduction in viscosity of the capsular fluid; the ciliation and movement of the early-stage veligers; the onset and termination of feeding on nurse eggs; the development of such structures as the larval kidneys, adult kidney, foot, operculum, tentacles, and eyes; the resorption of the velar lobes; and the dissolution of the capsular plug. These observations paralleled morphological descriptions of encapsulated development in *Nucella emarginata* by LeBoeuf (1971) and Lyons & Spight (1973), based on the removal

Table 1

Percentage of stripped and whole capsules in which embryos successfully completed development when cultured under two different conditions (autoclaved, antibiotic-treated seawater, and UV-sterilized seawater) in two separate experiments. n , number of capsule pairs used in each experiment.

Culture conditions	Ex-periment #	% successful development:		n	Date conducted
		Strip-ped	Whole		
Autoclaved, antibiotic-treated seawater	1	100	100	9	September, 1992
	2	35	100	23	July, 1993
	Overall	53	100	32	
UV-sterilized seawater	1	50	100	18	September, 1992
	2	38	100	40	September, 1993
	Overall	40	100	58	

of embryos from their capsules. The photographs in Figure 3 are thus the first to document the natural *intracapsular* development of *Nucella emarginata* embryos.

Embryos developing within stripped capsules suffered considerably higher mortality than embryos in whole capsules under both culture conditions (Table 1; Figure 4). Although embryos within all capsules reared in autoclaved, antibiotic-treated seawater survived in September 1992 (Table 1), under the same conditions in July 1993, there was a substantial increase in the mortality of embryos within stripped capsules. This appeared to be due to a flagellated protist that infected many cultures a few weeks after capsules had been stripped; these protists were never seen in my earlier 1992 cultures. Protists produced a mucous covering around the capsule and eventually managed to penetrate the inner capsule wall and feed on the developing embryos. Attempts to kill these organisms by periodically swabbing the exterior of infected capsules with 70% alcohol proved unsuccessful. The source of these protists was unclear, but it appears possible that protists were present on the capsule wall prior to stripping, and survived the initial swabbing with alcohol.

Embryos within stripped capsules also suffered higher mortality compared to those in whole capsules when cultured in UV sterilized seawater (Table 1; Figure 4). Again, mortality of these embryos appeared to result from the penetration of the capsule chamber by protists.

DISCUSSION

Attempts to rear neogastropod embryos outside their egg capsules have met with mixed success (Pechenik et al., 1984; Rivest, 1986). Embryos with relatively short encapsulated development times and a pelagic larval stage (e.g.,

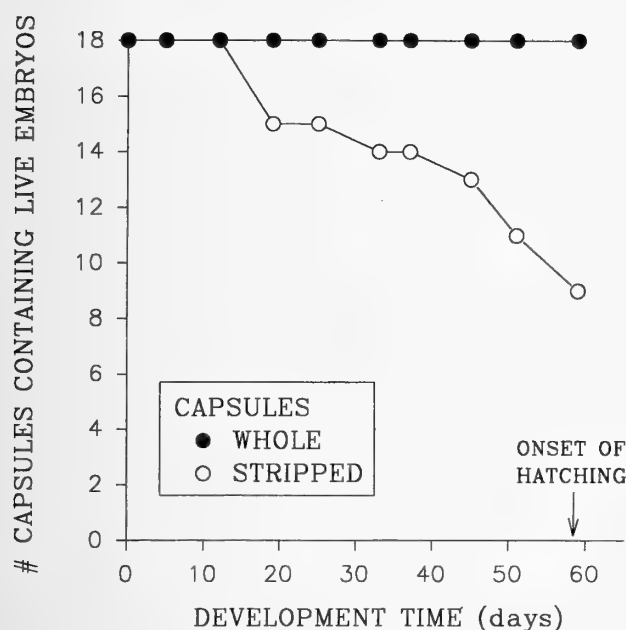


Figure 4

Number of stripped and whole capsules containing live embryos when cultured in UV sterilized seawater at 10–12°C from September–October 1992.

Ilyanassa obsoleta: Costello & Henley, 1971; *Conus* spp.: Perron, 1981) appear to survive well when cultured outside the confines of their capsule walls. However, those with longer term development, and enclosed with nurse eggs for nutrition, have typically suffered much higher mortality when removed from the capsule chamber. Pechenik et al. (1984) reported 95% mortality of early stage “excapsulated” embryos of the muricid snail, *Nucella lapillus*, over an 18 day culture period. Likewise, other studies have also failed to raise early-stage excapsulated embryos of this (Stöckmann-Bosbach, 1988) and other prosobranch gastropods (Rivest, 1986). In contrast, Lord (1986) was able to rear 35 pre-shelled embryos of *N. lapillus* over a 21 day period by culturing them within filtered, autoclaved, antibiotic-treated seawater; however, this experiment lasted for only a portion of the developmental period of this species. Although survival rates are undoubtedly higher for later-stage embryos removed from their capsules (Pechenik et al., 1984), embryonic mortality is not the only concern associated with culturing embryos outside their capsule chamber. For those embryos requiring extraembryonic nutrition during development, an artificial culture medium may not always provide embryos with the same accessibility to or the same concentration of nourishment. Consequently, the development of excapsulated embryos may not accurately reflect the normal encapsulated development of muricid gastropods.

Development of embryos within stripped capsules is clearly a useful alternative to raising embryos outside their

capsules. Embryos can be viewed through the inner capsule wall during development and still remain enclosed with albumen and nurse eggs in their natural fluid medium. Nevertheless, the high susceptibility of embryos within stripped capsules to contamination by bacteria and protists is still a cause for concern when using this technique. In the present study, embryonic mortality was directly related to the length of time embryos were cultured within stripped capsules (Figure 4), but differed little among the two culture treatments (Table 1). Contamination by protists thus may never be avoided with certainty, especially given that the source of the contamination might be the capsule wall itself. The probability of contamination of stripped capsules by protists can be reduced, however, by studying species with shorter development times than *Nucella emarginata*. Alternatively, if only one particular developmental stage is of interest, capsules could be stripped immediately prior to that stage. Clearly, therefore, the mortality of embryos within stripped capsules can be minimized without reducing this technique’s effectiveness.

Despite the high mortality of embryos enclosed within stripped capsules, embryos successfully developed through to hatching within 40 stripped egg capsules over a developmental period lasting as long as 77 days. Thus, for those species of muricid gastropods depositing embryos within opaque capsular cases, such as all five northeastern Pacific species of *Nucella* (e.g., *N. emarginata* [northern and southern species; see Palmer et al., 1990], *N. canaliculata*, *N. lamellosa*, and *N. lima*), this technique provides an effective means of viewing changes in the behavior and morphology of embryos during their intracapsular development. Given the structural similarity between the capsule walls of muricid gastropods and other neogastropod groups (e.g., the Buccinacea: D’Asaro, 1988), this technique may also be applied to other gastropod taxa enclosing developing embryos within multilaminated capsules.

Stripped egg capsules can also be used to address questions concerning the benefits and costs associated with the deposition of eggs within tough, thick-walled egg capsules. Chaffee & Strathmann (1984) have suggested that the rate of development of embryos enclosed within benthic egg masses may be constrained by the diffusion of oxygen into or metabolic wastes out of these structures. Recently, I have been able to test this by comparing the developmental rate of embryos enclosed within whole versus stripped capsules. My preliminary results have indicated that embryos in stripped capsules do indeed develop significantly faster than embryos in whole capsules (Rawlings, in preparation), thus suggesting that there is a substantial developmental cost associated with the deposition of embryos within thick-walled capsules.

I have also used stripped egg capsules to examine some of the benefits associated with the encapsulation of eggs. Gastropod egg capsules are generally assumed to be protective, but surprisingly few studies have attempted to determine what exactly capsules protect embryos from (see Pechenik, 1986, for a review). I have recently examined

the effectiveness of the capsule wall in resisting predators by comparing the resistance of whole and stripped capsules to intertidal isopods (Rawlings, in press). The low survival of embryos within stripped capsules in the present study is also a testament to the ability of the outer capsule wall to resist attack by protists that would otherwise consume these embryos. Stripped egg capsules may also help further our understanding of the role of the capsule wall in acting as an osmotic barrier to solute molecules, and as a filter for the penetrating rays of ultraviolet light. This technique thus has the potential, under controlled conditions, to be an invaluable tool in understanding more about the development of encapsulated embryos, and the benefits and costs associated with the deposition of eggs within thick-walled capsules.

ACKNOWLEDGMENTS

I would like to thank A. R. Palmer and L. Gosselin for critically reviewing earlier drafts of this manuscript, and K. Durante, L. Gosselin, and G. Jensen for their ideas and suggestions in helping to culture embryos successfully within stripped egg capsules. I am also grateful to the director and staff of the Bamfield Marine Station for making this research possible. This research was supported by a Bamfield Graduate Scholarship and a Province of Alberta Graduate Fellowship to T.A.R., and a NSERC operating grant to Dr. A. R. Palmer.

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Spawning Periodicity and Shell Microgrowth Patterns of the Venerid Bivalve *Phacosoma japonicum* (Reeve, 1850)

by

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Abstract. Reproductive cycle and shell microgrowth patterns of the venerid bivalve, *Phacosoma japonicum* (Reeve, 1850) from the Japanese coast were examined. In the population from Tokyo Bay, gonads of both male and female ripen between June and July, and spawning occurs during late June to early August. While shells of juveniles grow most rapidly between June and July, mature individuals suddenly cease shell growth just before spawning, and they resume shell growth just after spawning. This temporary cessation of shell growth produces a spawning break in the shell microstructure. After the onset of sexual maturity, spawning breaks appear annually. Similar results were obtained from the populations in Hakodate Bay (north Japan) and Kagoshima Bay (south Japan). These results indicate that spawning breaks may be useful in reconstructing sexual maturity patterns of extant and fossil bivalves.

INTRODUCTION

Analyses of life history patterns, such as early development, absolute growth, and reproduction in extant and fossil organisms, constitute an integral part of the understanding of evolution. Organisms with accretionary skeletons, such as bivalves, record life history information within their shell microstructure. As a result, comparative sclerochronological analysis of extant and fossil materials has proven to be valuable in paleoecological investigations (e.g., Rhoads & Pannella, 1970; Lutz & Rhoads, 1980; Jones, 1983).

Growth increments of bivalves are often well preserved in the outer shell layer. They can exhibit cyclical and interrupted growth incrementation (Kennish, 1980). In general, the cyclic growth pattern of increments reflects subdaily tidal, daily, fortnightly tidal, or annual periodicities. Of all the periodic structures recorded in the shell, annual increments have been recognized in most extant species and have been studied in detail for age and growth rate determinations in local populations under different environmental settings (e.g., Weymouth et al., 1931; Tanabe & Oba, 1988).

On the other hand, irregular growth breaks reflect periods of environmental or physiological stresses. In *Mercenaria mercenaria*, growth breaks are caused by freeze shocks (in winter), heat shocks (in summer), thermal shocks,

shell-margin abrasions, spawning, neap tides, and storms (Kennish, 1980). Spawning breaks in this species can be distinguished from the other types of growth breaks by the characteristic microstructure pattern observed in the outer shell layer, and appear annually after the onset of sexual maturity (Pannella & MacClintock, 1968; Kennish, 1980). Hence, spawning breaks are expected to represent a good indicator of sexual maturation for other extant bivalve species. Also, if these breaks can be distinguished in fossil shells, it becomes possible to estimate the age of sexual maturity in fossil bivalves.

The venerid bivalve *Phacosoma japonicum* (Reeve, 1850) is a common intertidal to subtidal species, inhabiting the coasts of Japan, Korea, and China (Habe, 1977). Fossils of this species are also found abundantly in the Pleistocene-Holocene marine deposits of the Japanese Islands (Takagi, 1986). The ease of access to a large quantity of samples, for both extant and fossil materials, as well as recent accumulation of knowledge about its life history make this species suitable for this study. Recent sclerochronological analysis of *P. japonicum* using marked and recovered specimens has revealed that large-scale repeated layers in this species are formed annually in winter, and they can be used for age and growth rate determinations (Tanabe, 1988). Using this approach, Tanabe & Oba (1988) demonstrated a latitudinal variation in the shell growth pat-

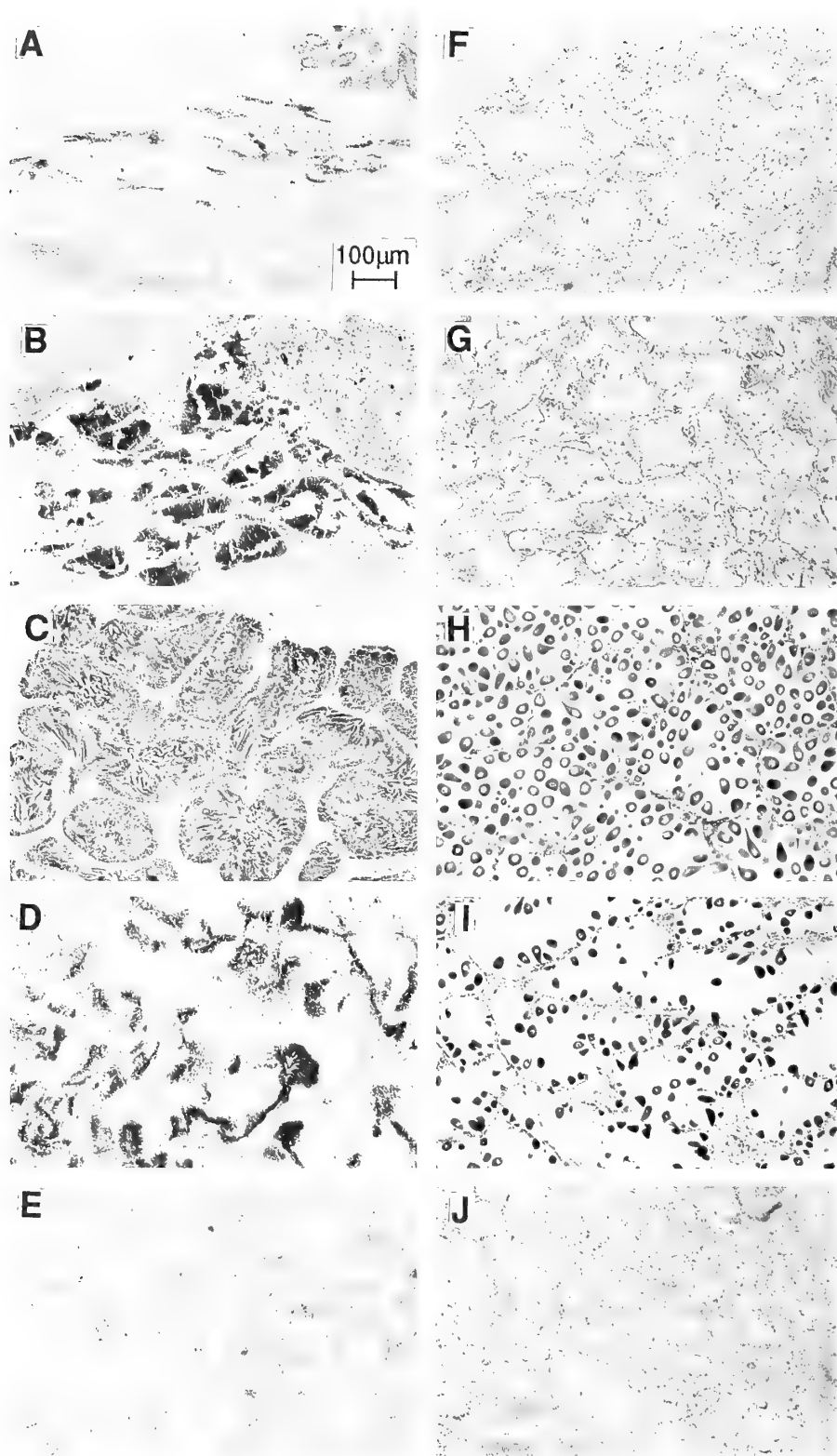


Figure 1

Optical photomicrographs of the sections of the male and female gonadal tissues in *Phacosoma japonicum* in each phase of the reproductive cycle. The scale bar in A pertains as well to B–J. All specimens were collected from

terns of this species, and Sato (1994) examined the relationship between shell growth and sexual maturation for a number of local populations of this species. These studies demonstrated that individuals from northern localities are characterized by later sexual maturation in their life, later offset of interval of shell growth, and larger shell size at a given age than those from southern localities.

The objective of this study was to delineate the relationship between shell microgrowth patterns and annual reproductive cycles in living *P. japonicum* and to describe spawning breaks in the shell microstructure of this species.

MATERIALS AND METHODS

Materials

Living individuals of *Phacosoma japonicum* were collected monthly between January 1992 and October 1992 from the intertidal sand flat of Nojima Coast, Tokyo Bay, central Japan (35°19'30"N, 139°38'40"E). They were analyzed for their shell microgrowth patterns and annual reproductive cycles.

Specimens from two other populations were also analyzed for their shell microgrowth patterns. They were collected in June 1992 from the subtidal sand flat of Kamiiso Coast, Hakodate Bay, northern Japan (41°49'N, 140°42'E), and the intertidal sand flat of Shigetomi Coast, Kagoshima Bay, southern Japan (31°42'30"N, 130°38'E). Living animals from the subtidal zone were recovered from commercial port landings, and those from the intertidal zone were sampled manually at low tide.

The shells of all the specimens utilized in this study are deposited at the University Museum, University of Tokyo (UMUT RM 19635, 19636, 19639).

Methods

The reproductive cycle of *Phacosoma japonicum* was examined in the population of Tokyo Bay. For this purpose, gonadal tissue in each specimen was excised and weighed using a dial scale (accuracy ± 10 mg). The dissected gonadal tissue was fixed for 48 hours in a solution of 10% formic acid diluted with seawater, followed by dehydration through a graded series of ethanols and benzols, and then embedded in paraffin (melting point: 58°C). Thin transverse sections of the gonadal tissue were prepared at intervals of 8 μ m thickness and were stained with hematoxylin-eosin. The stained thin sections were observed and photographed using an Olympus model AHBS-515 optical microscope.

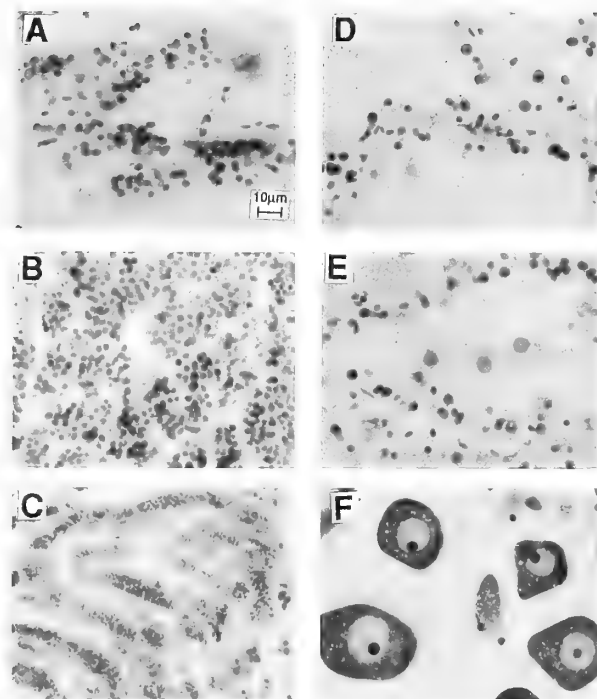


Figure 2

Optical photomicrographs of the sections of the germ cells of *Phacosoma japonicum*. The scale bar in A pertains as well to B–F. All specimens were collected from Tokyo Bay. A: Primary spermatocytes. A male collected on 9 April 1992. B: Secondary spermatocytes. A male collected on 6 May 1992. C: Spermatozoa. A male collected on 16 June 1992. D: Early oocytes. A female collected on 9 April 1992. E: Oocytes in the late active phase. A female collected on 6 May 1992. F: Free oocytes. A female collected on 16 June 1992.

Based on histological examination of thin-sectioned gonad, each specimen was assigned a specific gonad developmental stage; i.e., early active (EA), late active (LA), ripe (R), partially spawned (PS), and spent (S). The frequency of occurrence of each gonad developmental stage in monthly samples provided data on the temporal progression of the reproductive cycle. In addition, the mean gonad index [(gonad weight $\times 100$)/soft body weight] was calculated for sexually mature individuals to analyze the annual reproductive cycle of the population.

To examine the shell microgrowth patterns of *Phacosoma japonicum*, a single valve from each specimen was sectioned from the umbo to the ventral margin along the

← Tokyo Bay. A: Early active phase of a male collected on 9 April 1992. B: Late active phase of a male collected on 6 May 1992. C: Ripe phase of a male collected on 16 June 1992. D: Partially spawned phase of a male collected on 15 August 1992. E: Spent phase of a male collected on 15 August 1992. F: Early active phase of a female collected 9 April 1992. G: Late active phase of a female collected on 6 May 1992. H: Ripe phase of a female collected on 16 June 1992. I: Partially spawned phase of a female collected on 15 August 1992. J: Spent phase of a female collected on 15 August 1992.

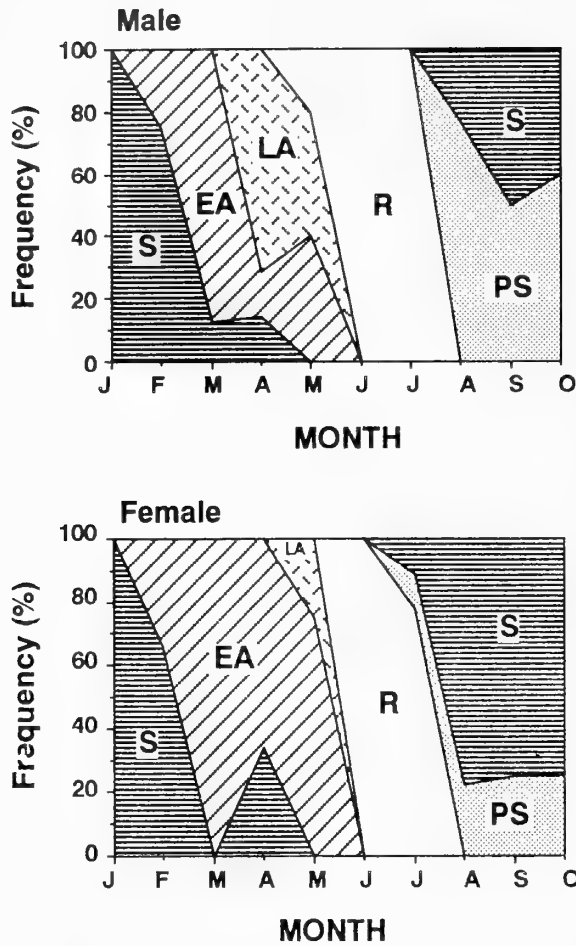


Figure 3

Frequency of occurrence of each phase of the reproductive cycle in monthly collected samples of *Phacosoma japonicum* from Tokyo Bay during January–October 1992. (EA) early active phase, (LA) late active phase, (R) ripe phase, (PS) partially spawned phase, and (S) spent phase.

axis of maximum growth. The sectioned valve was polished and etched with 5% acetic acid for 10 minutes, and then an acetate peel was prepared for each specimen by pressing a sheet of triacetylcellulose film (25 μm in thickness) on the etched surface flooded with acetone. Growth increments in each acetate peel were viewed by means of a Nikon V-16 profile projector at magnification, $\times 100$. The maximum width of each microincrement was measured successively from the umbo to the ventral margin using a digital micrometer (accuracy $\pm 1 \mu\text{m}$) attached to the profile projector.

Monthly shell growth patterns were analyzed based on the annual increments produced by freeze-shock (winter) breaks (cf. Tanabe, 1988). Shell heights from the umbo to the ventral margin of the annual increments were measured in each specimen using a slide caliper with an ac-

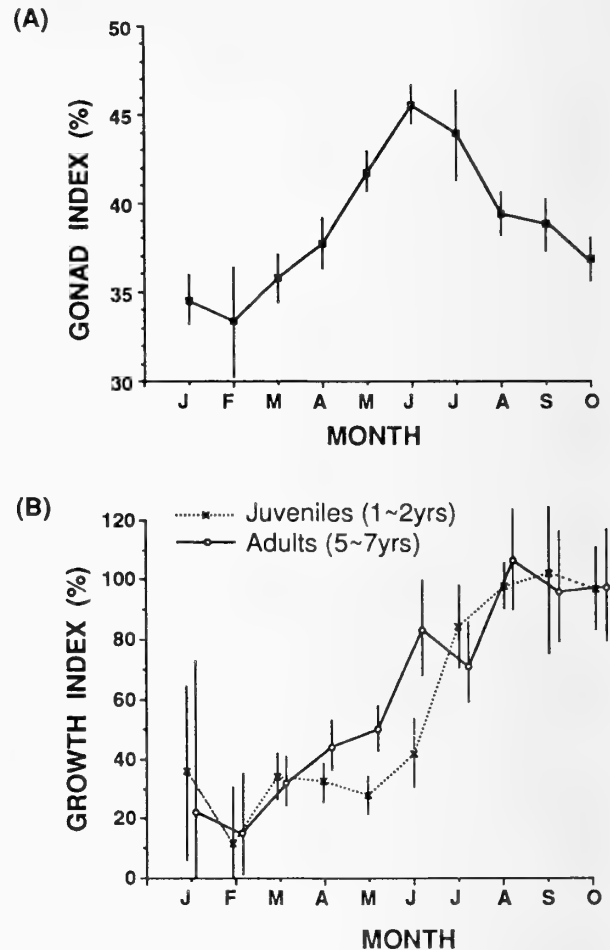


Figure 4

Relationships of seasonal development of gonads and monthly growth curve in the specimens of *Phacosoma japonicum* collected from Tokyo Bay during January–October 1992. A: Seasonal change in the mean gonad index [(gonad weight $\times 100$)/soft body weight]. Mean and the range of one standard deviation (vertical bar) are indicated, B: Monthly shell growth patterns of growth index (shell increment/the last winter break to the expected maximum shell growth) in juvenile and mature specimens. Mean and the range of one standard deviation (vertical bar) are indicated.

curacy of $\pm 0.05 \text{ mm}$. Net growth (x), defined as the increase of shell height in the period from the time of the last winter break to the month of sampling, was standardized for each individual of different age classes by the expected annual growth (y), defined as the distance from the last winter break to the expected next winter break (cf. Goshima & Noda, 1992). The extent of the expected annual growth (y) for each individual was estimated using the Ford-Walford plot equation (Ford, 1933; Walford, 1946). The equation is expressed as $H_{R+1} = aH_R + b$, where H_R is the shell height at the R th winter break (in mm), H_{R+1} is the shell height at the $R+1$ th winter break (in

Table 1

Regression constants for the Ford-Walford plot equations ($H_{R+1} = aH_R + b$), in *Phacosoma japonicum* from Tokyo Bay. Relating shell height (H_R , mm) at the R th winter break to shell height (H_{R+1} , mm) at the $R+1$ th winter break. a , b : constants, n : number of specimens, r : correlation coefficient.

R	$R+1$	a	b	n	r
1	2	1.517	0.651	205	0.552
2	3	2.411	0.346	151	0.660
3	4	2.083	0.533	137	0.744
4	5	1.127	0.820	116	0.785
5	6	0.131	1.048	76	0.868
6	7	0.081	1.038	37	0.929
7	8	0.216	0.997	16	0.942
8	9	0.584	0.916	3	0.994

mm), and a and b are constants determined by a simple regression between H_R and H_{R+1} of different individuals of the same sample. Using this equation, shell height at the expected next winter break of each individual (H_{R+1}) can be estimated by shell height at the last winter break (H_R) and constants at each age class (a , b). The ratio x/y is hereafter defined as the "growth index". It is very useful to analyze monthly growth patterns, because the relative extent of growth in each month can be compared among individuals of all different age classes.

RESULTS

The Reproductive Cycle of *Phacosoma japonicum*

Histological examination of gonadal tissue revealed that gametogenesis in *Phacosoma japonicum* is very similar to that in the Atlantic surf clam *Spisula solidissima*, which was analyzed in detail by Ropes (1968). Following the classification of gametogenesis proposed by Ropes (1968), the reproductive cycle of *P. japonicum* is described below.

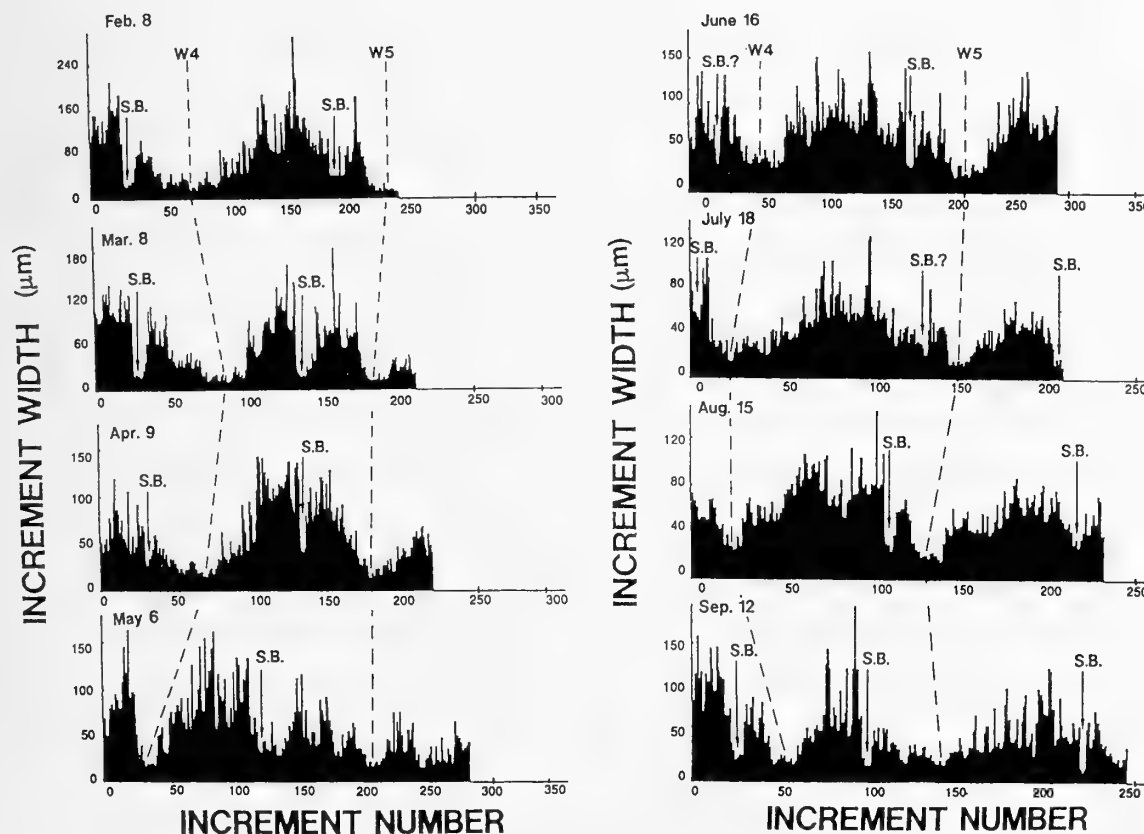


Figure 5

Shell microincrement growth patterns from the 4th winter break to shell margin in monthly collected specimens of *Phacosoma japonicum* from Tokyo Bay in 1992. The number of microincrements and width of each microincrement were measured in a specimen of each monthly sample. W4, W5: the 4th and 5th winter breaks, respectively. S.B.: spawning break. Winter and spawning breaks are fitted by eye.

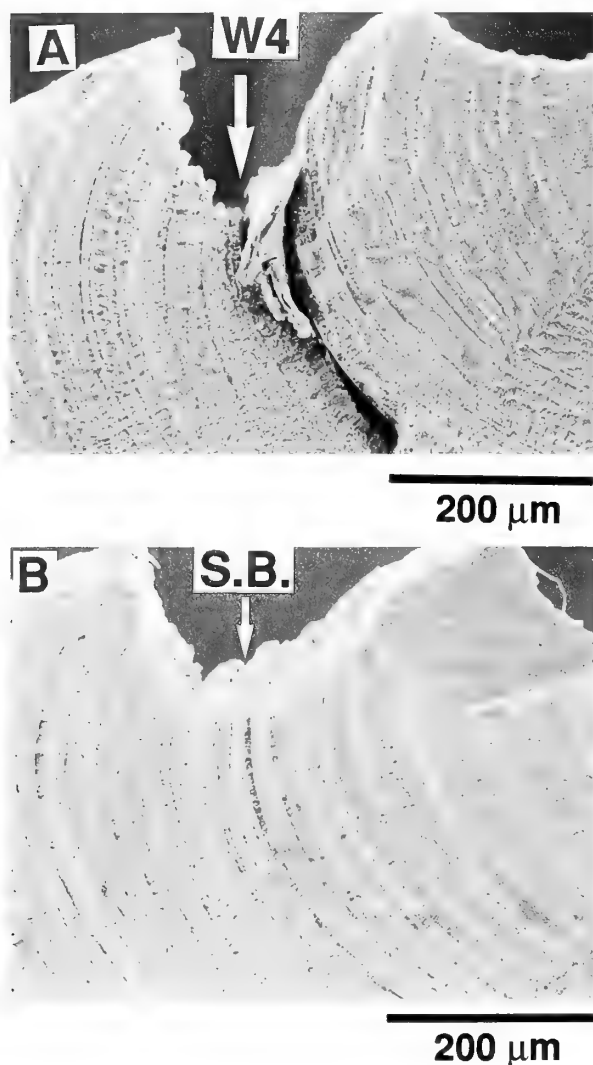


Figure 6

Scanning electron micrographs of the shell microgrowth sequence in the outer shell layer of *Phacosoma japonicum* collected from Tokyo Bay on 16 June 1992 (UMUT RM19636). A: The shell microgrowth sequence near the 4th winter break (W4). B: The shell microgrowth sequence near the spawning break (S.B.) in the 3rd annual increment.

Early active phase (Figure 1A, F): In this phase, primary spermatocytes proliferate toward the lumina from the alveolar walls in male gonads (Figure 2A), and the early oocytes appear at the periphery of the alveolar walls in female gonads (Figure 2D).

Late active phase (Figure 1B, G): Many secondary spermatocytes are seen in male gonads in the late active phase (Figure 2B). On the other hand, oocytes in the late active phase in female gonads are larger than early oocytes, and many are round in shape (Figure 2E).

Ripe phase (Figure 1C, H): In this phase, spermatozoa or free oocytes occupy a major space in the gonadal tissue. Only mature sperm is termed spermatozoa. The head of each sperm is about $2.5\ \mu\text{m}$ in length and cone-shaped (Figure 2C). Male gonads in the ripe phase consist of dense masses of spermatozoa in the alveoli. Free oocytes are characterized by their separation from the lumina of the alveoli in female gonads (Figure 2F). Each oocyte contains a nucleus measuring about $20\ \mu\text{m}$ in diameter which is surrounded by voluminous vitelline material. The diameter of the vitellus is about $40\ \mu\text{m}$. Each nucleus possesses a small opaque basophilic nucleolus measuring about $5\ \mu\text{m}$ in diameter.

Partially spawned phase (Figure 1D, I): Some spermatozoa or free oocytes remain in the lumina of some alveoli of partially spawned specimens.

Spent phase (Figure 1E, J): The alveoli of spent specimens contain few or no spermatozoa or oocytes. The lumina of these individuals are characteristically open.

Seasonal variation in the frequency of the occurrence of each phase in the reproductive cycle of *Phacosoma japonicum* collected from Tokyo Bay in 1992 is shown in Figure 3. In both males and females, gonads recover and grow between January and May. Ripening continued throughout the limited interval during June to July. Some individuals had begun to spawn in July, and all the individuals were either partially spawned or spent between August and October. After spawning, many males were partially spawned, whereas most females were spent (Figure 3). The mean gonad index increased from February to June, and decreased from July to October (Figure 4A). Therefore, the spawning season of *P. japonicum* in Tokyo Bay is considered to be summer, between late June and early August.

Monthly Shell Growth

Figure 4B shows monthly shell growth patterns observed in *Phacosoma japonicum* from Tokyo Bay, based on the growth index calculated from the Ford-Walford plot equations (Table 1). Immature individuals (1 to 2 years-old) usually grow more rapidly between June and July than any other seasons. However, mature individuals (5 to 7 years-old) grow gradually between February and June, slow or cease growth between June and July, and then resume growth from July to August (Figure 4B). In *P. japonicum*, the monthly growth rate of adults stagnates in the spawning season.

Shell Microgrowth Patterns

Monthly shell microgrowth patterns were examined in 5 year old male specimens collected from Tokyo Bay (Figure 5). The 4th and 5th winter breaks (W4 and W5 in Figure 5) are easily recognized in all specimens, because

Table 2

Distribution of spawning breaks in each age class of specimens of *Phacosoma japonicum* collected monthly from Tokyo Bay in 1992.

Specimen no.	Sampling date	Shell height (mm)	Age	Sex	Gonad stage	Spawning breaks in each age class						
						1	2	3	4	5	6	7
HR9202-08	Feb. 8	41.85	5	M	EA	—	—	++	+			
HR9202-09	Feb. 8	39.80	5	M	EA	—	+	++	+			
HR9203-04	Mar. 8	46.10	5	F	EA		—	+	+			
HR9203-12	Mar. 8	43.50	5	M	EA	—	—	+	+			
HR9204-14	Apr. 9	42.35	5	F	EA		—	+	+			
HR9204-18	Apr. 9	44.60	5	M	LA		—	++	+			
HR9205-12	May 6	44.00	5	F	LA		—	—	+			
HR9205-14	May 6	44.55	5	F	LA		—	+	+			
HR9206-02	June 16	48.40	5	M	R		—	+	+			
HR9206-06	June 16	45.40	5	F	R	—	+	+	+			
HR9207-05	July 18	45.05	5	M	R			+	++	(+)		
HR9207-06	July 18	46.10	5	M	R		—	+	+	(+)		
HR9207-07	July 18	45.05	5	M	R		—	+	+	(+)		
HR9207-09	July 18	44.20	5	M	R	—	—	++	++	(+)		
HR9207-11	July 18	38.70	4	F	R	—	—	+	(+)			
HR9208-02	Aug. 15	51.10	7	F	S		—	—	+	+	+	(+)
HR9208-12	Aug. 15	51.30	6	M	PS		—	+	++	++	(++)	
HR9208-16	Aug. 15	44.40	4	F	S		—	+	(+)			
HR9208-17	Aug. 15	46.40	5	M	PS		—	+	++	(+)		
HR9208-18	Aug. 15	44.30	4	M	PS		—	+	(+)			
HR9209-07	Sep. 12	46.65	5	F	S			+	+	(+)		
HR9209-08	Sep. 12	45.05	5	M	PS	—	—	—	+	(+)		
Frequency of individuals with spawning breaks (%)						0	14.3	87.0	100	100	100	

M: male; F: female.

EA: early active phase; LA: late active phase; R: ripe phase; PS: partially spawned phase; S: spent phase.

+: one spawning break in the age class; ++: more than two spawning breaks in the age class; —: no spawning breaks in the age class; (+), (++) : spawning breaks between the last winter break and ventral shell margin.

microincrement width decreases when approaching the break and increases after passing the break (cf. Tanabe, 1988:fig. 2). Recent sclerochronological analysis has demonstrated that microincrements of *Phacosoma japonicum* do not coincide with subdaily tidal or daily growth increment, and the number of microincrements per annual increment is not fixed among specimens (Tanabe, 1988). Comparison of the shell microgrowth patterns among monthly collected specimens reveals that the number of microincrements after the 5th winter break rapidly increases from April to June, and that the width of each increment becomes greatest in June (Figure 5). However, the microincrement width suddenly decreases in July, and a spawning break (S.B. in Figure 5) is formed at this time. After the formation of a spawning break, the microincrement width increases again in August and thereafter gradually decreases in September.

Figure 6 illustrates scanning electron micrographs of the microincrement sequence in a specimen collected on 16 June 1992, in which winter breaks and spawning breaks are observed. The winter break is characterized by a deep V-shaped notch in the outer shell layer (Figure 6A). This

break can be distinguished on the shell surface. The spawning break is preceded by little or no reduction in the thickness of microincrements and is followed by a series of thin microincrements that reflect reproductive stresses (Figure 6B). A V-shaped notch does not appear at the spawning break. Hence, this break is rarely discernible on the shell surface. Spawning breaks in *P. japonicum* can be distinguished from winter breaks and other types of growth breaks by their characteristic shell microgrowth patterns. For example, freeze-shock and heat-shock breaks are preceded by a slow decrease in the thickness of microincrements, but spawning break does not yield such a slow decrease of shell growth. Thermal-shock, abrasion, neap-tide, and storm breaks are followed by a rapid increase in the thickness of microincrements, but spawning break is followed by slow recovery. Moreover, only spawning break always occurs at around the widest increments produced in the summer season.

Spawning breaks occur annually after the 3rd winter break in most specimens of *Phacosoma japonicum* from Tokyo Bay (Table 2). This is consistent with the observation of gonadal development in this population which

Table 3

(A) Distribution of spawning breaks in each age class of selected specimens of *Phacosoma japonicum* from Hakodate Bay. Sampling date: June 26, 1992. (B) Distribution of spawning breaks in each age class of selected specimens of *P. japonicum* from Kagoshima Bay. Sampling date: June 4, 1992.

(A)																	
Specimen no.	Shell height (mm)	Age	Sex	Spawning breaks in each age class													
				1	2	3	4	5	6	7	8	9	10	11	12	13	
NH-626	60.70	13	M	—	—	—	—	++	++	—	++	+	+	+	+		
NH-627	59.40	6	M	—	—	—	+	+									
NH-628	64.50	7	F	—	—	—	+	+	+								
NH-629	62.95	11	F	—	—	—	+	+	+	—	+	+	+				
NH-630	56.00	7	F	—	—	—	+	+	—								
NH-631	61.10	11	M	—	—	—	—	+	—	—	+	+	+				
NH-632	59.30	6	M	—	—	—	++	++									
NH-633	71.30	12	F	—	—	+	+	+	+	—	—	—	—	—			
NH-634	66.70	12	F	—	—	—	+	+	+	+	+	—	+	+			
NH-635	72.90	12	F	—	—	+	+	+	+	+	+	+	—	+			
NH-636	58.40	8	F	—	+	—	+	+	—	+							
NH-637	68.50	14	M	—	—	—	++	+	—	+	—	+	+	—	++	—	
NH-638	70.10	13	M	—	—	—	—	+	+	—	—	+	+	+	—		
NH-639	65.05	8	F	—	—	—	—	+	—	+							
NH-640	58.20	7	F	—	—	—	—	—	—								
NH-641	57.60	6	F	—	—	—	+	+									
Frequency of individuals with spawning breaks (%)				0	6.3	12.5	68.8	93.8	53.8	60.0	62.5	75.0	75.0	66.7	66.7	0	

(B)										
Specimen no.	Shell height (mm)	Age	Sex	Spawning breaks in each age class						
				1	2	3	4	5	6	
SG-101	50.00	6	F	—	+	+	+	+		
SG-102	44.35	4	M	+	+	+	+			
SG-103	43.40	4	M	—	+	+				
SG-104	42.00	4	F	+	+	+				
SG-105	40.50	4	F	—	+	+				
SG-106	40.50	4	F	—	+	—	+			
SG-107	39.50	4	M	—	—	+	++			
SG-108	39.00	4	F	—	+	+				
SG-109	38.40	4	M	—	++	++				
SG-201	42.75	6	M	—	+	++	+	+		
SG-202	42.80	5	F	+	+	+	+			
SG-203	44.00	4	M	—	+	+				
SG-204	44.90	5	F	—	+	+	+			
SG-205	44.85	4	F	+	+	—				
SG-206	42.80	6	M	—	+	+	+	+		
SG-207	41.40	4	M	—	++	+				
SG-208	40.80	5	M	—	++	+	+			
Frequency of individuals with spawning breaks (%)				23.5	94.1	88.2	100	100		

Vertical rule: the age class in which spawning breaks already appeared in more than 50% of the specimens.

attains sexual maturity at 3 years of age (Sato, 1994). A good correlation between the age of first appearance of spawning breaks and the age of sexual maturity was also observed in the samples from two other geographically isolated populations (Table 3). In the population from

Hakodate Bay characterized by later sexual maturation (Sato, 1994), spawning breaks first appear at a later age class, whereas in the population from Kagoshima Bay, characterized by earlier sexual maturation, spawning breaks first appear at an earlier age class. In both Kagoshima and

Hakodate samples, the age class, in which spawning breaks had already appeared in more than 50% of the specimens, is equal to the age of sexual maturity (4 years of age for the Hakodate, and 2 years of age for the Kagoshima population: Sato, 1994).

Most mature individuals from Tokyo Bay begin to form a spawning break at their shell margin in July. However, at that time they do not yet begin to spawn, and their gonads remain in the ripe phase of the reproductive cycle (see Table 2). In August, most mature individuals have completed spawning, and some broad increments following the spawning break were secreted in their shell margins. Orton (1926) and Coe (1948) noted that many bivalve species suddenly stop feeding at the time of spawning, resulting in a drastic decrease in shell growth. Spawning breaks in *Phacosoma japonicum*, however, begin to develop just before the time of spawning; after spawning, microincrement growth recovers rapidly.

After the onset of sexual maturity, spawning breaks in *Phacosoma japonicum* generally occur once a year. Male specimens, however, occasionally produce more than two spawning breaks per year in every sample examined (Tables 2 & 3). In August, many males from Tokyo Bay were in the partially spawned phase of the reproductive cycle, whereas most females from the same area were in the spent phase (Figure 3). These data suggest that many males cannot release all gametes in their gonads at one spawning event, whereas most females can do it, at least in the population from Tokyo Bay.

Many individuals from Hakodate Bay do not develop spawning breaks after about 6 years of age (Table 3). However, microscopic observations of the gonads revealed that all specimens older than 6 years of age have innumerable free oocytes or spermatozoa in their gonadal tissues in June (Sato, 1994). As the number of shell microgrowth increments formed during a year tends to decrease with age (Tanabe, 1988; Tanabe & Oba, 1988), spawning breaks in individuals older than 6 years of age may not have preserved in the microgrowth sequence as a result of shell dissolution during the winter season (Tanabe & Oba, 1988).

DISCUSSION

Annual increments have been distinguished in a number of bivalve species and have been used for age and growth rate determination (see Table 4). In most species, annual increments are produced by freeze-shock breaks or heat-shock breaks. The season of annual increment formation is different among species and even among local populations in the same species. In *Macoma balthica*, annual increments are produced by freeze-shock breaks in most local populations (Bachelet, 1980), but in the population from the Wadden Sea, heat-shock breaks are produced annually (Lammens, 1967). In *Mercenaria* spp. from the East Coast of North America, annual increments are produced in winter in northern populations (e.g., Kennish & Olsson,

1975; Kennish, 1980; Jones et al., 1989) and during summer in southern populations (Jones et al., 1990).

Spawning breaks are also used to assess annual incrementation in some species (e.g., *Cryptopecten vesiculosus*, Hayami, 1984; *Pecten irradians*, Gutsell, 1930; *Spisula solidissima*, Jones et al., 1978; *Arctica islandica*, Thompson et al., 1980). It may be possible to assess the age of sexual maturity in these bivalves, based on the growth increments. However, spawning breaks in these species were recognized merely as internal or external growth bands, and the difference from other growth breaks was not clarified.

Spawning breaks in the shell microgrowth pattern have been studied in detail in *Mercenaria mercenaria* (Pannella & MacClintock, 1968; Rhoads & Pannella, 1970; Cunliffe & Kennish, 1974; Kennish & Olsson, 1975; Kennish, 1978; Kennish, 1980). The mode of development of spawning breaks in *M. mercenaria* described by these authors is very similar to that in *Phacosoma japonicum*; i.e., in both species, the sequence of wide microincrements produced in the summer season is abruptly interrupted by a spawning break and immediately followed by a sequence of thin microincrements. Therefore, spawning breaks in the two species can be distinguished from other types of growth breaks.

Pannella & MacClintock (1968) and Rhoads & Pannella (1970) reported that in *Mercenaria mercenaria* from the east coast of North America, spawning breaks do not develop until the bivalve attains sexual maturity at the age of 2 years. In *Phacosoma japonicum*, spawning breaks also occur annually after the age of sexual maturity in the three populations analyzed (Tables 2 & 3). The correlation between the age of first appearance of spawning breaks and the age of sexual maturity observed in *M. mercenaria* and *P. japonicum* indicates that spawning breaks are effective for determining the age of sexual maturity in extant populations of these two species, and could possibly be applied to fossils as well.

According to Pannella & MacClintock (1968), specimens of *Mercenaria mercenaria* from the east coast of North America occasionally produce more than two spawning breaks per year, and males typically exhibit more spawning breaks than females. Since growth declines at the time of spawning, at the same age, males are generally smaller than females in the same population of *M. mercenaria*. By contrast, spawning breaks in *P. japonicum* occur once a year in many males and most females (see Tables 2 & 3). Hence, the average shell height at a given age does not differ between them. But male specimens were rarely observed to produce more than two spawning breaks per year in the populations studied. The number of spawning breaks per year, therefore, may be useful for sex determination of extant and fossil specimens in these species.

Spawning breaks and winter breaks are preserved in Pleistocene fossil specimens of *Phacosoma japonicum* (Sato, in preparation). Analysis of shell microgrowth patterns in these fossil bivalves should be valuable in delineating their sexual maturity patterns.

Table 4
Bivalve species whose annual increments have been documented.

Species	Locality	Season annual increments appeared	Spawning season	Reference
<i>Mytilus edulis</i>	Damariscotta River, Maine, U.S.A.	Dec.-May (F.B.)		Lutz (1976)
<i>Modiolus (M.) modiolus</i>	Strangford Lough, North Ireland	winter (F.B.)	summer	Seed & Brown (1978)
<i>Cryptopecten vesiculosus</i>	Sagami Bay, central Japan	summer (S.B.)	summer	Hayami (1984)
<i>Pecten irradians</i>	Beaufort, North Carolina, U.S.A.	fall (S.B.)	fall	Gutsell (1930)
<i>Pecten maximus</i>	The Isle of Man, U.K.	Mar.-May (F.B.)	Apr.-Sep.	Mason (1957)
<i>Pecten magellanicus</i>	Gulliver Cove, Bay of Fundy, Canada	Feb.-Mar. (F.B.)	Aug.-Sep.	Stevenson & Dickie (1954)
<i>P. (Mizuhopecten) yessoensis</i>	Lake Saroma, Hokkaido, Japan	June-Sep. (S.B.) & Feb.-Mar. (F.B.)	May-June	Maru & Obara (1967)
<i>Cerastoderma edule</i>	Thames Estuary, U.K.	winter (F.B.)	June-July	Farrow (1971)
<i>Clinocardium californiense</i>	Hakodate Bay, Hokkaido, Japan	Sep. (H.B.?)	May	Goshima & Noda (1992)
<i>Fuluvia mutica</i>	Seto Inland Sea, western Japan	Apr.-Jan. (F.B. and S.B.)	Apr.-May & Sep.-Oct.	Inoue (1955)
<i>Pseudocardium sachalinensis</i>	Aniwa Bay, Saghalien, Russia	summer (H.B. or S.B.) & winter (F.B.)	June-July	Yamamoto (1947)
<i>Spisula solidissima</i>	Chinotengue Inlet, Virginia, U.S.A.	late summer (S.B.)	late summer	Jones et al. (1978)
<i>Peronidia venulosa</i>	Shiriuchi, Hokkaido, northern Japan	Sep.-Jan. (S.B. and F.B.)	Sep.-Oct.	Goshima et al. (1991)
<i>Macoma balthica</i>	Gironde Estuary, SW France	Jan.-Feb. (F.B.)	May-July & Sep.-Nov.	Bachelet (1980)
	Wadden Sea, Netherlands	late summer (H.B.)	Mar.-Apr.	Lammens (1967)
<i>Scrobicularia plana</i>	Conway Bay, North Wales, U.K.	winter (F.B.)	Aug.-Sep.	Hughes (1970a, b)
<i>Siliqua patula</i>	Pismo, California-Chignik Bay, Alaska	winter (F.B.)		Weymouth et al. (1931)
<i>Arctica islandica</i>	Long Island, New York, U.S.A.	late summer (S.B.)	late summer	Thompson et al. (1980)
<i>Corbicula sandai</i>	Lake Biwa, Shiga, central Japan	June (S.B. or H.B.) & Dec.-Feb. (F.B.)	May-June	Furukawa (1953)
<i>Corbicula fluminea</i>	Raritan River, New Jersey, U.S.A.	winter (F.B.)		Fritz & Lutz (1986)
<i>Corbiculina leana</i>	Lake Suwa etc. Nagano, central Japan	winter (F.B.)	May-Aug.	Kawashiri (1948)
<i>Chamelea gallina</i>	Mediterranean Sea, Cullera, eastern Spain	Aug.-Oct. (H.B.)	June-July	Ramón & Richardson (1992)
<i>Tivela stultorum</i>	Pismo, California, U.S.A.	Nov.-Feb. (F.B.)	June-Dec.	Hall et al. (1974)
<i>Mercenaria mercenaria</i>	Barnegat Bay, New Jersey, U.S.A.	winter (F.B.)	summer	Kennish & Olsson (1975)
	Atlantic Coast, Florida, U.S.A.	late summer and fall (H.B.)	spring	Jones et al. (1990)
<i>M. campechiensis</i>	Gulf Coast, Florida, U.S.A.	late summer and fall (H.B.)	spring	Jones et al. (1990)
<i>Phacosoma japonicum</i>	Seto Inland Sea, western Japan	Dec.-Feb. (F.B.)	June-July	Tanabe (1988)
<i>Gemma gemma</i>	Indian Cove, Connecticut, U.S.A.	winter (F.B.)		Tevesz (1972)

Table 4
Continued.

Species	Locality	Season annual increments appeared	Spawning season	Reference
<i>Ruditapes philippinarum</i>	Lake Akkeshi, Hokkaido, Japan	winter (F.B.)	July–Sep.	Yamamoto & Iwata (1956)
<i>Callista chione</i>	Adriatic Sea, Grado, Italy	July–Oct. (H.B.?)	fall	Hall et al. (1974)
<i>Mya arenaria</i>	Hakata Bay, western Japan	winter (F.B.)	Oct.–Nov.	Goshima (1982)
	Prince Edward Island, Canada	late spring (F.B.?)	early June–mid. Aug.	MacDonald & Thomas (1980)

(F.B.): freeze-shock break; (H.B.): heat-shock break; (S.B.): spawning break.

ACKNOWLEDGMENTS

The author thanks Kazushige Tanabe (University of Tokyo), Michael J. Kennish (Rutgers University), and Kazuyoshi Endo (University of Tokyo) for critical reviews of the manuscript and for valuable comments. Thanks to Yuji Taya (Nippon Dental University) and Takashi Noda (Hokkaido University) for instruction of histological techniques, and to Seiji Goshima (Hokkaido University) for his help in collecting samples. Two anonymous reviewers made helpful comments for improvement of this paper.

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NOTES, INFORMATION & NEWS

**Chemoattraction and Dietary Preferences of
Helisoma trivolvis (Gastropoda: Planorbidae)
for Leaf Lettuce and Tetramin**

by

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Introduction

Numerous studies are available on chemoattraction and dietary preferences of the medically important planorbid snail *Biomphalaria glabrata* (Say, 1818) for various food items (Uhazy et al., 1978; Thomas & Assefa, 1979; Kpikpi & Thomas, 1992; Masterson & Fried, 1992; Marcopoulos & Fried, 1993). Less information on food preference is available for other planorbid snails, although Boland & Fried (1984) examined chemoattraction of a Pennsylvania strain of *Helisoma trivolvis* (Say, 1816) to romaine lettuce (*Lactuca sativa longifolia*). The present study was concerned with chemoattraction and dietary preferences of a Colorado strain of *Helisoma trivolvis* for iceberg leaf lettuce (*Lactuca sativa*) and Tetramin® (fish food). The Colorado strain of *H. trivolvis* is refractory to infection with larval trematodes, lacks melanin, has an orange-red body, and has been used extensively in neurobiology studies (see Park et al., 1991). Since planorbid snails in the genus *Helisoma* may be useful in the biological control of schistosome vectors such as bulinid and biomphalarid snails, information on the food-locating ability of planorbid snails is important.

Materials and Methods

Stock cultures of *Helisoma trivolvis* (Colorado strain) were maintained in the laboratory on a mixed diet of iceberg leaf lettuce (*Lactuca sativa*) and Tetramin (TetraWerke, Melle, Germany) (Park et al., 1991). The bioassay chamber for the chemoattraction studies consisted of 100 × 15 mm petri dishes (Masterson & Fried, 1992). Two parallel lines were drawn 2.8 cm apart on the bottom of each petri dish to produce three zones (A, B, C). The side zones (A and C) each had an area of 14.1 cm², and the middle zone (B) had an area of 20.0 cm² (Masterson & Fried, 1992). Fifty-five mL of artificial spring water (Cohen et al., 1990) was added to each petri dish. The snails were placed into the petri dish 10 min after the food or food extracts to allow diffusion of the potential chemoattractants (Masterson & Fried, 1992). The dishes were maintained at 22 ± 1°C on a level work bench under overhead diffuse fluorescent light (Marcopoulos & Fried, 1993). Ten petri dishes were used for each trial.

Snails were 11 ± 1 mm in shell diameter and were maintained without food for approximately 3 hr prior to each trial. For each trial, a single snail was placed in the center of zone B in the bioassay chamber described above. Pieces of filter paper (1 cm²) were impregnated with food extracts (experimentals) or chloroform (controls) and placed at the edges of zones C and A, respectively. The pieces of filter paper were allowed to air dry prior to introducing them into the petri dish bioassay, and were held in place in the dish by paper clips (Marcopoulos & Fried, 1993).

Lettuce and Tetramin were extracted in chloroform-methanol (2:1) as described by Boland & Fried (1984) to obtain lipophilic and hydrophilic fractions for use in the bioassay studies on chemoattraction to either lipophilic or hydrophilic extracts (see Table 1). About 25 µL of each fraction was placed on a filter paper square.

For 50 min, at intervals of 5 min, the zone in which the snail was located was recorded (a total of 10 observations per snail). A control group was used in each trial. It consisted of blanks in place of food or extracts in order to observe the random movements of the snails. Random observations based on blank experiments were used as the expected values to calculate the chi-square value in each experimental design. A *P* value of < 0.05 was considered

Table 1

Dietary preferences and chemoattraction of snails for leaf lettuce and Tetramin.

Experiment	Percentage of snails in zones			Chi- square	<i>P</i>
	A	B	C		
Dietary preferences					
Bl vs. Bl	41	21	38	—	—
Bl vs. L	12	6	82	115.87	< 0.0001
Bl vs. T	2	9	89	128.70	< 0.0001
L vs. T	31	6	63	66.93	< 0.0001
Chemoattraction to lipophilic extracts					
Bl vs. Bl	39	23	38	—	—
Bl vs. LL	12	18	70	45.79	< 0.0001
Bl vs. TL	3	11	86	94.73	< 0.0001
Chemoattraction to hydrophilic extracts					
Bl vs. Bl	40	22	38	—	—
Bl vs. LH	21	21	58	11.05	0.004
Bl vs. TH	0	42	58	10.66	0.005

Bl = blank; L = lettuce; T = Tetramin; LL = lettuce lipophilic; LH = lettuce hydrophilic; TL = Tetramin lipophilic; TH = Tetramin hydrophilic.

significant. Each experiment was done 10 times for every group.

Results and Discussion

The results of the dietary preference and chemoattraction studies are presented in Table 1. Snails were significantly attracted to either lettuce or Tetramin. Given a choice between these foods, snails were significantly attracted to Tetramin. Snails were significantly attracted to the hydrophilic extracts of either lettuce or Tetramin; they were very significantly attracted to the lipophilic extracts of lettuce or Tetramin.

Results of our work are remarkably similar to previous findings of *Biomphalaria glabrata* that showed that this biomphalarid preferred Tetramin over leaf lettuce and that single snails were significantly attracted to both hydrophilic and lipophilic extracts of leaf lettuce and Tetramin. Some differences are apparent between the Pennsylvania and Colorado strains of *Helisoma trivolvis* because Boland & Fried (1984) showed that the Pennsylvania strain was significantly attracted to the hydrophilic rather than the lipophilic portion of leaf lettuce in a two-choice design. Some of these differences may be related to the fact that Boland & Fried (1984) used romaine lettuce in their study and we used iceberg lettuce in our study.

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Western Society of Malacologists Annual Meeting

The twenty-eighth Annual Meeting of the Western Society of Malacologists will be held at the resort at Chena Hot Springs, near Fairbanks, Alaska, from June 2 to June 6, 1995. The agenda will include contributed papers on all areas of molluscan studies—freshwater, marine, and terrestrial, living and fossil. Symposia on ecology and paleoecology are being organized with the help of Howard Feder and David Hopkins. Also in the planning stages are an auction, reprint sale, and banquet. The University of Alaska Aquatic Collection will be available for visitors before and after the meeting. For more information, contact WSM President, Nora R. Foster, University of Alaska Museum, 907 Yukon Drive, Fairbanks, Alaska 99775, USA. Phone: (907) 474-9557. E-Mail: FYAQUA@aurora.alaska.edu. Or contact Conference and Special Events, 117 Eielson Building, University of Alaska, Fairbanks, Alaska 99775.

Western Society of Malacologists in conjunction with the Santa Barbara Malacological Society and the Northern California Malacozoological Club are offering a Student Research Grant in Malacology

As part of their commitment to the continued study of mollusks, the Western Society of Malacologists, the Santa Barbara Malacological Society, and the Northern California Malacozoological Club are pleased to announce the availability of grants to support student research in malacology. Funds are available for actual research costs, including but not limited to, field and laboratory equipment, chemicals, photographic supplies, computer time and supplies, microscope usage fees, and reasonable research travel costs.

Eligibility: Applicant must be a full time student in a formal graduate or undergraduate degree program.

The thesis, dissertation, or research project must be focused primarily on the systematics, ecology, physiology, biochemistry, or paleontology of marine, terrestrial, or freshwater mollusks. Research currently in progress or beginning in the 1995-1996 academic year will be considered.

Requirements: Six copies of the following documents are required for each application:

1. A completed application form.
2. A proposal, limited to two pages, which discusses the research project and its malacological significance, including details of the work to be aided by this grant.
3. A budget which outlines how the grant funds will be used.

4. A resume or outline of the applicant's academic background.
5. A letter of recommendation from the applicant's research advisor (original and five copies to be sent separately by advisor).
6. A list of grants and amounts that are currently being received or have been applied for for the 1995–1996 academic year.

Award: Research grants up to \$1000 are available.

Application deadline: Completed applications must be received no later than May 1, 1995. Awards will be announced by July 31, 1995. Please send applications to: Malacology Grant, Department of Invertebrate Zoology, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, California 93105, USA. For further information or an application form contact: Paul Scott at (805) 682-4711, ext. 319 (voice); (805) 563-0574 (fax), or inverts@sbmnh.rain.org (Internet). When requesting an application form by mail, please include a stamped, self-addressed envelope.

Indo-Pacific Malacological Meeting Preliminary Notice

The Council of the Malacological Society of Australasia has agreed to hold an international meeting on mollusks of the Indo-Pacific region in Perth, Western Australia in January or February 1997. This notice is intended to alert malacologists worldwide of the upcoming meeting and to solicit suggestions for possible symposia. All suggestions of possible topics are welcome. The meeting will include all aspects of malacology, including mollusks of marine, freshwater, and terrestrial habitats. If sufficient interest develops, a postconference field trip to the southwest of Western Australia can be arranged. As plans develop, the conference will be advertised in malacological journals. To

be placed on the list for direct receipt of future notices please write to: Dr. F. E. Wells, Western Australian Museum, Perth 6000, Western Australia (Fax: 61-9-328-8686).

International Commission on Zoological Nomenclature

The following applications were published on 30 September 1994 in Volume 51, Part 3 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2866—MEGALODONTIDAE Morris & Lycett, 1853 (Mollusca, Bivalvia) and MEGALODONTIDAE Konow (Insecta, Hymenoptera): proposed removal of homonymy.

Case 2902—*Acanthoteuthis* Wagner in Münster, 1839 and *Kelaeno* Münster, 1842 (Mollusca, Cephalopoda): proposed conservation of usage.

Case 2904—*Nesopupa* Pilsbry, 1900 (Mollusca, Gastropoda): proposed conservation.

The following Opinions concerning mollusks were published on 30 September 1994 in Volume 51, Part 3 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1779. *Potamolithus* Pilsbry & Rush, 1896 (Mollusca, Gastropoda): placed on the Official List with *Paludina lapidum* d'Orbigny, 1835 as the type species.

Opinion 1780. *Turbo politus* Linnaeus, 1758 (currently *Melanella polita*; Mollusca, Gastropoda): usage of the specific name conserved, so conserving the specific name of *Buccinum acicula* Müller, 1774 (currently *Ceciloides acicula*).

BOOKS, PERIODICALS & PAMPHLETS

Fossil Shells from Oregon Beach Cliffs

by ELLEN J. MOORE. 1994. Chintimini Press, Corvallis, Oregon. 88 pp. \$9.95 + \$2.00 shipping. (Chintimini Press, 3324 SW Chintimini Avenue, Corvallis, OR 94333)

On a local scale, public curiosity about mollusks is not great enough to create a market for expensive identification guides and handbooks. There is, however, a large population of the "casually interested" who may find their curiosity piqued by a day at the shore and a hand full of shells from beach drift or fossil shells from a sea cliff. Regional field guides are not the answer for an outing at a local beach. And coffee table books are designed to decorate coffee tables. There is a major need for affordable local guides, and a tremendous opportunity to educate and stimulate public interest in all aspects of biological diversity through such publications.

Ellen Moore has devised a marvelous solution in the form of an attractive and stimulating handbook, produced and marketed from her own home press. There are a number of respects in which this handbook might serve as an exemplar for anyone interested in a similar educational undertaking. It is in this sense that it deserves more than casual review.

(1) It assumes no prior knowledge of mollusks, fossils, geology, nomenclature, or classification. It provides a skeletonally simple background in all of these that can be read and absorbed quickly. It resists the temptation to overwhelm.

(2) It is a guide to what a local resident or tourist is most likely to see. It can be carried on an outing, and it contains simple field excursions that are tempting in their challenge to follow a map and find the geologic features and fossils that are described.

(3) The photographs of fossils are of high quality (many are recognizable from Moore's 1963 USGS Professional paper 419 on the mollusks of the Astoria Formation). They are typical specimens, easily matched to the common fossils in the sea cliffs, with no need for keys or technical vocabulary.

(4) The text contains human interest elements such as references to Native American uses of mollusks and the contents of shell middens in coastal marine terrace deposits. The author is also aware of the draw of curious modes of fossil preservation in noting that weathered concretions containing *Patinopecten* specimens are locally known "clam burgers."

(5) The author's love of the Oregon coast is clear and contagious!

Professional scientists owe more of this kind of effort to the public. This guidebook stimulates me to think more deeply about additional ways to challenge and engage local

residents and tourists. Might we be able to find ways to encourage less collecting and more observation: to share the joys of comparing, counting, measuring, tabulating, photographing, drawing? Can we do a better job of popularizing the importance of fossils in reconstructing the history of life? Can we make mollusks just as interesting as dinosaurs? Can we take advantage of more opportunities to create an awareness of conservation issues and the scope and importance of biological diversity?

Carole S. Hickman

Third California Islands Symposium: Recent Advances in Research on the California Islands

edited by F. G. HOCHBERG. 1994. Santa Barbara Museum of Natural History: Santa Barbara, California. xiv + 661 pp. \$40.00 plus tax and shipping.

In March 1987 the Santa Barbara Museum of Natural History hosted the third in a series of symposia devoted to the islands off southern California and the outer coast of Baja California, Mexico. These islands have long held a fascination for researchers in geology, geography, history, anthropology, and terrestrial and marine botany and zoology. Since the first Channel Islands symposium in 1965, an increasing number of agencies, academic institutions, and commercial scientific organizations have become involved in investigations on the islands.

Of the 47 papers included in this volume, mollusks figure most prominently in the following: Temporal and spatial variation in the recruitment of the sea hare, *Aplysia californica*, at Santa Catalina Island, California, by S. C. Penning; Geographic variation in population characteristics of an intertidal gastropod [*Littorina keenae*]: demographic differences or settlement history?, by R. J. Schmitt; Rocky intertidal community structure on Santa Barbara Island and the effects of wave surge on vertical zonation, by R. R. Seapy and M. M. Littler; Rocky intertidal macroinvertebrates of the Southern California Bight: an overview and checklist, by Seapy and Littler; Dynamics and distribution of black abalone populations at San Nicolas Island, California, by G. R. Van Blaricom; Prehistoric predation on black abalone by Chumash Indians and sea otters, by W. J. Douros; and The occurrence of red abalone shells in northern Channel Island archaeological middens: implications for climatic reconstruction, by M. A. Glassow. Other ecological, geological, and anthropological articles also mention mollusks.

Biologists who work on the Channel Islands will prob-

ably enjoy, as I did, reading the papers on history—a reminder that in so many ways, these islands are “so near and yet so far” from the urban mainland of southern California.

B. Roth

Results of the first two Channel Islands symposia are published in the following:

- Philbrick, R. N., ed. 1967. Proceedings of the Symposium on the Biology of the California Islands. Santa Barbara Botanic Garden: Santa Barbara, California. 363 pp.
- Power, D. M., ed. 1980. The California Islands: Proceedings of a Multidisciplinary Symposium. Santa Barbara Museum of Natural History: Santa Barbara, California. 787 pp.

A Review of the North American Freshwater Snail Genus *Pyrgulopsis* (Hydrobiidae)

by ROBERT HERSHLER. 1994. Smithsonian Contributions to Zoology No. 554. 115 pp., 53 figures.

Robert Hershler's latest Smithsonian monograph is one of the most significant works on North American freshwater mollusks to appear in many years. The small spring snails composing *Pyrgulopsis* are widely distributed throughout the central part of the continent, particularly in the United States. With 65 described species and many more yet to come, the genus is rivaled in diversity in the U.S. freshwater mollusk fauna only by *Elimia*. Over half of the described forms presently have conservation significance, either as federal listed or candidate taxa. Several are known to be extinct or near extinction. Many occur in only one or a few springs, often in especially isolated areas of the West. Hence, the accumulation of anatomically useful topotypes for 60 of the taxa was no mean feat in itself.

Hydrobiidae have been a major focus of freshwater malacology in Australia, Europe, the U.S., and elsewhere for the last 20 years. In the Americas this is exemplified particularly by the efforts of Hershler, G. M. Davis, F. G. Thompson, and D. W. Taylor. Both higher and species-level taxonomy is in a state of flux. The rapid pace of change can be gauged easily from this work, which includes some 32 species described since 1985, 22 by Hershler and his collaborators. Generic concepts have evolved comparably. Burch (1989, *North American Freshwater Snails*. Malacological Publications: Hamburg, Michigan) listed 26 of the taxa covered by Hershler here. Only five species (and one synonym) were included by Burch in *Pyrgulopsis*. Hershler differs considerably from previous authors in his concept of the genus; e.g., he subsumes *Marstonia* Baker, 1926; *Fontelicella* Gregg & Taylor, 1965; *Savaginius* Tay-

lor, 1966; *Apachecoccus* Taylor, 1987; and *Yaquicoccus* Taylor, 1987. Given the number of undescribed species (perhaps another 65) and the apparent mosaic nature of character distribution and evolution in these snails, generous definition of *Pyrgulopsis* probably is justified. It is possible, however, that several species groups eventually will be formally recognized. Equally significant changes in interpretation and content of other North American freshwater Hydrobiidae [*Tryonia*, *Fluminicola*, the Cochliopinae (e.g., Hershler & Thompson, 1992, Malacol. Rev. Supp. 5:140 pp), and the Amnicolinae] have occurred recently or are forthcoming. In this and other efforts, Hershler has managed to resolve in a few years many of the nagging problems of U.S. hydrobiid taxonomy. At the very least, *Amnicola lustrica* Pilsbry, 1890, should at last have a stable residence!

This work has the excellent anatomical drawings and SEM photographs that are hallmarks of Hershler's previous hydrobiid papers. Both are closely coordinated with the text, and scale is indicated on each. The emphasis on morphology of the distal female genitalia (in addition to male) is notable, as is the use of opercular and radular features. Shell characters are also excellently described and illustrated, and it is made abundantly clear how difficult identification of these small snails would be on conchological features solely. The style is very clear, consistent, and concise, almost to the point of being telegraphic. Especially useful and uncommon features are the lists of incorrect and fossil ascriptions to *Pyrgulopsis*, but given the number of taxa and synonyms involved, a taxonomic index would also have been useful. Also very valuable is the cladistic phylogeny of the completely characterized species. This is also quite succinctly stated and explicated, and enlargement of this treatment in the future would be helpful. Certain of the species groups previously recognized as genera or subgenera, as well as one or two others, seem likely to remain both monophyletic and distinct even if species diversity doubles. One particularly interesting finding is the apparent cohesiveness of the basic eastern and western U.S. divisions, despite considerable enlargement and redefinition of both.

A feature that I missed from some of Hershler's previous works (e.g., Hershler & Sada, 1987, Proc. Biol. Soc. Washington 100:776–843; Hershler, 1989, Proc. Biol. Soc. Washington 102:176–248; Hershler & Pratt, 1990, Proc. Biol. Soc. Washington 103:279–299) was a discussion of zoogeography of the genus and its relation to past drainage history. Avoidance of *ad hoc* scenarios in biogeography is difficult at best, but these snails are particularly amenable to more rigorous attempts. Many of the hypotheses put forward by Taylor (1985, Evolution of freshwater drainages and molluscs in western North America. Pp. 265–321 in C. J. Smiley (ed.), *Late Cenozoic History of the Pacific Northwest*. Pacific Division AAAS & California Academy of Sciences: San Francisco), for example, can now be retested or corroborated from much new evidence. Hershler evidently intends this monograph to be a summary of prog-

ress to date and a basis for future, more detailed revision. It serves both purposes well, and should also be of exceptional interest to conservation biologists and private collectors, as well as to specialists. Because of the condensed style, readers unfamiliar with these snails may need to refer to the earlier Hershler papers cited above for background.

Single copies of this work may be ordered from: Federal Series, Smithsonian Institution Press, 470 L'Enfant Plaza, Suite 7100, Washington, D.C. 20560.

T. J. Frest

Molluscan Microscopic Anatomy

Microscopic Anatomy of Invertebrates, Volume 5, Mollusca I. edited by FREDERICK W. HARRISON and ALAN J. KOHN. Wiley-Liss, Inc., New York. 390 pp. \$185.00.

Microscopic Anatomy of Invertebrates (MAI) is one of the most ambitious and philosophically coherent compilations of data on the invertebrate phyla. For those who already own and consult encyclopedic molluscan references such as the *Treatise on Invertebrate Paleontology*, the molluscan volumes of the multi-volume *Reproduction of Marine Invertebrates*, and especially the multi-volume treatise *The Mollusca*, there may be concerns about overlap in scope and redundancy of coverage.

I want to dispatch these concerns immediately by noting the dedication of this series (a) to the inclusion of new data, (b) to a predominantly *functional* interpretation of structure, and (c) to a primary focus on form and function at the cellular and ultrastructural level.

Molluscan biologists and paleobiologists who do not normally read broadly outside of malacological journals will find this volume especially enlightening in its coverage of a large body of elegant and important research using mollusks as model organisms or model systems. Although there is a long tradition of molluscan functional anatomy that is rooted in a comparative systematic context, it has been oriented more toward the whole organism and its component systems, investigated above the cellular level of structure and above the physiological level of function.

For those accustomed to working in a comparative context, this volume will not be easy to mine for comparative data. At the same time, it has much to reveal to the comparative/systematic biologist who wishes to pinpoint fundamental gaps in knowledge. One of the great challenges of comparative biology is that of incorporating the data of microscopic anatomy in phylogenetic analysis. Comparative studies of cellular and biochemical processes in mollusks are time-consuming, and the techniques are not normally part of the training of systematists. However, much of the excitement of this volume lies in the glimpse of how

much better we would understand molluscan microanatomy and physiology if we investigated it systematically and, conversely, how much better our understanding of relationships would be if we could obtain more comparative ultrastructural and physiological data at the level of cellular and biochemical processes.

Four major molluscan groups are treated in the volume: aplacophorans, polyplacophorans, prosobranchs, and opisthobranchs. The aplacophoran chapter (Amélie Scheltema, Martin Tscherkassky, and Alan Kuzirian) and the polyplacophoran chapter (Douglas Eernisse and Patrick Reynolds) are especially welcome contributions in the amount of previously unpublished data and number of new transmission and scanning electron micrographs. Both are a blend of review and substantial primary research, and both address questions of the functional meaning of structure. These chapters convey the clear impression that a much greater proportion of total research effort has been devoted to microscopic anatomy than is the case with gastropods. The aplacophoran chapter is especially impressive in the amount of original illustration: it includes more than 100 transmission electron micrographs and micrographic illustration of 11 species that have not been illustrated previously.

The prosobranch chapter (Janice Voltzow) is the centerpiece of the volume and by far the most rich in its detail and scholarship (141 pages and 832 literature citations). Nearly one-third (31%) of the literature reviewed in this chapter has been published within the past 10 years, and it is interesting to note that the citations from this period are evenly divided between molluscan (127 citations) and non-molluscan (128 citations) journals and references. There are more than 100 line drawings that are either original or redrawn. The innovative treatment of the structure, organization, and role of gastropod connective tissue and musculature is especially welcome as is the treatment of the integration of structure and function in the gastropod foot. This chapter is the most successful in emphasizing the functional interpretation of structure. It consistently points to studies of taxa and structural complexes that serve well as models for integrative understanding of the organism.

The opisthobranch chapter (Terry Gosliner) is least successful in meeting the objectives of the series, adopting a phylogenetic rather than a functional perspective. It is unfortunate that a more appropriate author was not secured for the task. The chapter not only lacks ultrastructural detail, but, more significantly, it fails to provide a functional perspective. As a systematist, Gosliner is concerned not with the *meaning* of a structure but with whether, in a comparative sense, it is homologous or analogous, present or absent, primitive or derived. It is a valuable compilation, but it belongs somewhere else.

The excitement of this volume lies in the wealth of dynamic structural and ultrastructural data, presented not as a source of characters but as the basis for understanding molluscan function—the organism. It serves as a healthy

reminder to those who conduct their research within a systematic and phylogenetic framework that history is but one property of the organism. Achievement of a unified organismic point of view—an organismic paradigm—is, and always has been, *the* most fundamental goal of biology. And the problem of structure is historically the core problem of biology. Accordingly, organic form and function are the central reality of biology. Mollusks continue to play an important role as models in understanding the organism.

Mollusks serve as models in two senses: many species have properties that make them invaluable as *model taxa* for laboratory and field studies and many complex or uniquely molluscan features (e.g., radula, ctenidium, mantle, podocytes) that serve as *model systems* for addressing questions that span biological sub-disciplines and transcend mollusks.

In summary, in its structural and functional emphasis, this volume takes a refreshingly direct and dynamic view of the organism.

Carole S. Hickman

Reply by Terrence M. Gosliner

Professor Hickman seems to think that my contribution to the first molluscan volume of the *Microscopic Anatomy* series lacks ultrastructural detail and a functional perspective. While I certainly am of the opinion that my contribution contains much new information about opisthobranch ultrastructure and function, I want to focus my response on what I believe to be a far more important philosophical issue.

Dr. Hickman correctly states that I am not concerned with the "meaning of a structure but with whether . . . it is homologous or analogous, present or absent, primitive or derived." On the other hand, she criticizes a phylogenetic approach as providing a narrow perspective to problems of comparative biology. She believes that "organic form and function are the central reality of biology" and that "an organismic paradigm . . . is . . . the most fundamental goal of biology." This is an essentialist point of view that was popular with biologists in the early nineteenth century and exemplified by the works of Baron Cuvier. This approach fundamentally changed with the publication of Darwin's work in 1859. With the understanding that all life was descended from a single common ancestor, biology changed in most people's minds. Understanding how patterns of structure and function change over time, within and between lineages, is now the central principle of biology.

It is useful to study structure and function in the absence of phylogenetic information, just as the Chilton Auto Repair Manual allows one to fix and reassemble the motor

of a car. What makes comparative biology with a phylogenetic perspective different is that it permits one to study how the structures and corresponding functions of organisms change over time, in response to changing environments.

Dr. Hickman is correct in stating that I am concerned with homology and direction of change. Homology is essential to our understanding how structure and function change. For example, most gastropods have a structure called a bursa copulatrix. In most gastropods, this structure receives sperm during copulation. In most opisthobranchs, this structure also has the function of dissolving and resorbing the waste products of reproduction. In many cases, the structure in opisthobranchs is called a gametolytic gland. If we did not establish the homology and direction of evolutionary change of this structure, we would simply know that most gastropods have a bursa copulatrix and most opisthobranchs have a gametolytic gland with a different function. What makes this more informative is the additional information that the bursa copulatrix of most gastropods has been modified in opisthobranchs with corresponding changes in both structure and function.

While phylogenetic information is not the only important thing in biology, it is the only road map we have to make sense out of otherwise confusing differences in structure and function.

Terrence M. Gosliner

Bigger Blue

British Prosobranch Molluscs. Their Functional Anatomy and Ecology by VERA FRETTER and ALASTAIR GRAHAM. Ray Society Publication, Volume No. 161. August 1994. xix + 820 pp., 343 figs. ISBN 0 903874 23 7. Price £83.00 (US\$132.80).

The worker who can read again those opening lines ("The Mollusca are one of the great groups of the animal kingdom. . .") without a prickling of the skin has not yet achieved her maturity as a malacologist. Thirty-plus years of advances in gastropod biology have not diminished the stature of *British Prosobranch Molluscs*, first published in 1962 as Ray Society Publication No. 144.

Nevertheless (and helping to keep much of this big blue book from becoming a dated curiosity), authors Fretter and Graham have provided a revised and updated edition of their classic work. Vera Fretter was able to work on the revision up to and including the galley proof stage of production before her death in October 1992.

It is still big, and still blue. The typeface has changed from Roman to a businesslike Optima, but the familiar, sharp, informative drawings remain—perhaps even slightly more accessible because printed on more opaque stock. The illustrations in the newly added chapters are of the

same high quality. The revised edition is organized in two parts. Part I (chapters 2–22) contains most of the original text, with some deletions (molluscan radiation outside the gastropods; the physiology and biochemistry of shell secretion; prosobranch parasites; the appendices on classification, habitats and distribution). Part II (chapters 23–36) contains predominantly new material. The introduction (chapter 1) addresses material contained in both parts. Other parts of the original text have been either extended or replaced and appear in Part II (toxoglossan alimentary anatomy and feeding; the endocrine, excretory and vascular systems; most of the ecology; prosobranch classification and relationships). There are now two bibliographies, one for Part I and one for Part II; counting by bibliography pages, one-fourth again as many references are cited in the new Part II as in Part I. The systematic and author indexes of the first edition are gone, and likely to be missed. Elements of the original work regarded by the authors as well covered in other recent publications or peripheral to the main theme of the book have been deleted. Other parts have been rewritten in light of newly discovered facts and emerging concepts.

Users of the first edition will already realize that the title understates the scope of the work. Many of the studies cited involve other geographic areas (including the tropical Pacific and the west coast of North America), the terrestrial and freshwater environments, and, where pertinent, pulmonate and opisthobranch gastropods, chitons, and monoplacophorans. There are few other places to find so much basic information about gastropods under one cover: a good investment for general zoology libraries. As with the first edition, the prose is eminently readable (those who enjoy opening, say, *Moby Dick* at random and rereading whatever passage presents itself, for the pleasure of insights missed the last time through, will find *British Prosobranch Molluscs* similarly rewarding). Varying results of different authors and open questions are generally presented evenhandedly—although partisans in some of the more vigorously contested subject areas, such as alimentary system evolution, may not see it that way.

The two-part structure of the book means that it has to be used with caution. The chapters of Part I, being largely verbatim reprints of the first edition, sometimes, but not always, point to updated material in Part II. Tables of cross references at the ends of Part II chapters refer only to citations elsewhere in Part II. Fully integrating recent findings into the original text would have been a tremendous task; but many workers will probably consider adding xeroxed-and-pasted-up versions of chapters of interest to their own notebooks.

The otherwise high standards seem to have been changed for the last chapter (“The Relationships and Classification of Prosobranchs”)—undoubtedly the weakest and potentially most misleading part of the book. One way for the critic to deal with it would be simply to note that systematics is not Fretter and Graham’s strong suit—indeed, they basically end up (p. 737) endorsing the conclusions of Cox

(1960) and Hickman (1988) that a phylogenetically based classification is either impossible or inexpressible in the current language of taxonomy—and to suggest that the scholar look elsewhere. I will spend a little more time on it than that, first, because readers may tend to grant this chapter the same level of authority as the rest of the book; and, second, because in treating phylogeny as an appendix or afterthought to biology, it highlights the most significant criticism to be made of *British Prosobranch Molluscs* as a whole. The fundamentally distinct activities of systematics and classification (de Queiroz, 1988; O’Hara, 1993) are mingled in this chapter, and I shall not try to tease them apart.

Fretter and Graham tip their hand early (p. 724), stating that the goals of classification are “making identification easier” and “at a less practical level” suggesting relationships and evolutionary pathways. It is hard to imagine an understanding of classification more different from my own. Identification of taxa is independent of classification (unless we are speaking of the trivial way in which taxa could be classified on the basis of size, color, or the grace with which they move to “Dance of the Hours”). Pyramidellids did not suddenly become easier to identify when they were moved from Prosobranchia to Opisthobranchia. The characters by which one identifies a taxon may not be (and cannot exclusively be) the ones used in assigning it to more inclusive groups.

Moreover, a phylogenetic hypothesis (and its taxonomic expression) is not “less practical,” but, rather, essential if there is to be meaningful discussion of how observed differences in ecology, morphology, behavior, or distribution came about (Brooks & McLennan, 1991; O’Hara, 1992). To its credit, *British Prosobranch Molluscs* is practically free of those commonly encountered small narratives, sometimes with an overlay of adaptive “explanation,” that seek to place evolution of an attribute in a historical/ecological context. But in malacology at large, there is very little asking whether the attribute in question is novel with the taxon under discussion or is shared with other taxa through common ancestry. The null hypothesis in such cases is not “they don’t have [the attribute]” but “they have it because their ancestors had it.” This type of question can be investigated only in the context of an established phylogeny (O’Hara, 1988).

The authors’ dicta about classification say nothing about one of its aims being to enable us to make predictions. Nor do they seem to recognize that, because of the fact of organic evolution, the classification that affords the best predictive basis is the one most fully grounded in phylogeny (Hennig, 1966).

The updating of this section takes in recent taxonomic work impacting on the classification of prosobranchs (by Haszprunar, Lindberg, and Salvini-Plawén among others) but not current methodologies. Although they refer to torsion as “in the language of cladistics, a synapomorphy” of the Gastropoda (p. 724), the authors give no indication that they have considered the parsimony-driven, hypoth-

esis-generating forms of analysis used in phylogenetic systematics. Like the practitioners of canonical systematics, they continue to regard taxonomy as a process of *a priori* picking and choosing of characters for grouping ("taxobases"), with taxonomic decisions based on magnitude of difference criteria, e.g.: "Epitoniids and janthinids, though possessing shells of widely different appearances, are *sufficiently alike* in anatomy (though some resemblances may be merely adaptive convergence) to suggest that they . . . fall into a single superfamily, Epitonioida or Janthinoidea" (p. 736; emphasis supplied). They misrepresent the methods and focus of several taxonomists by claiming, for example, that two groups formerly in Archaeogastropoda (patellogastropods and neritimorphs) have been stated by their most recent students to be *so unlike the others* that they should be classified separately (contrast the actual basis used, for example, by Lindberg, 1988).

The special concerns of this chapter are enumerated (p. 725) as: "the validity of an archaeogastropod taxon," "what animals may be included in it and their relationships," "the nature of groups lying at the archaeogastropod-caenogastropod boundary," and "to what prosobranch groups the opisthobranch-pulmonate line may perhaps be related." The ways in which these concerns are pursued constitute a textbook example of the devices listed by O'Hara (1992) as harmful to the representation of evolutionary history: recognition of paraphyletic taxa, pruning of side branches, sequencing (as if in time) of contemporary taxa, and differential resolution of different parts of the tree.

After a review of other work, Fretter and Graham conclude (p. 733) that it is best to allow Archaeogastropoda to persist in prosobranch classification as a paraphyletic group; this gesture "has the apparent advantage of retaining a familiar taxonomic scheme." Of the alternatives, they object to representation of Patellogastropoda, Cocculiniformia, Vetigastropoda, and Neritimorpha as distinct and coordinate groups on the grounds that this constitutes "taxonomic inflation."¹ They regard it as unacceptable and extreme "to find sufficient common fundamental features to justify the belief that the four groups form a natural group of related animals" although admitting that "this is the traditional view" (p. 733). Having thus established that Archaeogastropoda properly refers to a grade, not a clade, Fretter and Graham are free to refer to an "archaeogastropod-caenogastropod boundary." Predictably, they find a number of groups that do not comfortably fit in either realm (e.g., Neritimorpha). The classification of such untidy groups is said to be dependent on taxobases, with the result that, "according to one's choice of criterion the boundary drifts raggedly from one position to another" (p. 733).

On p. 737 they draw a similar image of the relation

between prosobranch and opisthobranch realms, with various heterogastropod taxa "interpreted as forms which have failed to make the full journey from prosobranch to opisthobranch but represent important and suggestive staging posts on the way followed by those others that completed it successfully." Of course, only hindsight enables the authors to speak of "the full journey." A sense, like this, of completeness or destiny can easily arise in evolutionary narrative because the end point is known and all that precedes the end point can be viewed teleologically (O'Hara, 1992).

Here as elsewhere there is excessive emphasis on "mainstream prosobranch evolution" (that is, the sequence from archaeogastropod to caenogastropod—"mainstream" perhaps because well represented in the British fauna), in effect pruning the branches that do not lead to this perceived culmination. Calling heterogastropod evolutionary pathways "failures" represents the view through a particular set of lenses. A Permian malacologist would no doubt take a different view; and if after Earth's next round of mass extinction, the most extensive prosobranch re-radiation involves the descendants of *Architectonica*, the more parochial malacologists of that era may tend to regard Heterogastropoda as the "main line," and their big blue book contain a very different set of examples.

The chapter ends with a consideration of the Valvatidae, a group that defies neat pigeonholing in Fretter and Graham's scheme because "all its known members are restricted to fresh water, a fact that fits ill with their supposedly primitive evolutionary position" (p. 739). This is a problem only if one tries to sequence contemporaneous taxa from "primitive" to "advanced." In a more narratively neutral representation of evolutionary history, taxa are not referred to as primitive or derived or higher or lower; the terms primitive and derived are reserved for character states (de Queiroz, 1988; O'Hara, 1992). Similar sequence-thinking also shows up elsewhere in the book, as on p. 599 with the concern at which "level" within mesogastropods the neogastropod stock arose. The attitude which allowed the authors to write in the first edition of limpets being "amongst the more lowly members" of Prosobranchia (p. 448)—an assessment that witnesses to the territorial battles of *Lottia gigantea* will find hard to accept—has not been purged from the revised edition.

The Fourth Grievous Sin, differential resolution of different parts of the tree, is largely built in by the terms of the work: British *prosobranch* mollusks; and as a pulmonate specialist I was glad to be spared similar discussion of my specialty.

On balance, then, thirty-five thirty-sixths of *British Prosobranch Molluscs* merit a warm recommendation. The fact that "relationships and classification" are not estimated from a modern analytical perspective and better integrated into the whole is the reason this review remains two-hearted. The compendium of gastropod knowledge that effectively incorporates phylogeny and its taxonomic expression remains to be written.

¹ Taxonomic inflation, that bugbear of canonical systematics, would be a better metaphor if there were some external, objective measure of the value of the formal rank of a taxon analogous to purchasing power in economics. (There is none.)

The book can be ordered from Intercept Limited, P.O. Box 716, Andover, Hants., SP10 1YG, U.K. Tel: +44 (264) 334748. FAX: +44 (264) 334058.

B. Roth

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Neogene Paleontology in the Northern Dominican Republic 15.

The Genera *Columbella*, *Eurypyrene*, *Parametaria*, *Conella*, *Nitidella*, and *Metulella* (Gastropoda: Columbellidae)

by PETER JUNG. 1994. Bulletins of American Paleontology. 106 (344):1-45.

This monograph is the fifteenth contribution to the Dominican Republic ("D.R.") Project, the first of what I hope will be many international multidisciplinary paleontological studies modeled after the Deep Sea Drilling Project. This project, begun in 1977, is focused on the Neogene marine deposits of the Cibao Valley, in the Northern Dominican Republic, and is aimed at providing complete and detailed documentation of the geology and stratigraphy of the sequences, as a background for detailed taxonomic studies of the associated megafossil fauna. The deposits contain a highly diverse, continuous, and well-preserved marine fauna exposed in several locations, and are crucial to understanding the complex biological history of the Neogene Caribbean Basin. Much of the fauna had been published in the early 1900s; the ages and correlations of the sequences from which the fossils were taken, however, had never been rigorously established. Peter Jung, the author of this paper, is also one of the D.R. Project

founders, and has authored or co-authored three of the other monographs, including the original geological survey paper and two of the following taxonomic monographs, on the columbellid *Strombina* group and the cancellariids. He is now involved in a similar project with the Smithsonian Tropical Research Institute, to study the Neogene history of the Isthmus of Panama.

This particular paper is exclusively a taxonomic treatment, as was intended by the project directors; each of the (more than 40) specialists writing about the D.R. megafauna has only a small portion of the material to contend with. The project authors intend that a summary report will be published following the systematic monographs, to reconstruct paleocommunities and lay out the project's overall conclusions. Thirteen species from six columbellid genera are discussed in this paper; three species and one subgenus (which includes two extinct and apparently endemic Dominican species) are described as new, and two unknown forms are identified by open nomenclature, as the author justifiably felt that there were too few representative specimens of each at hand to describe them as new species at present. The six genera included herein do not represent an evolutionary grouping within the Columbellidae, and Jung has not suggested any such connections among them.

The systematic descriptions of the thirteen taxa are quite thorough. Several of the included species were represented in the D.R. sections by only a few specimens, and Jung provides complete descriptions of all material available as well as a discussion of any occurrences of the taxa in other parts of the Caribbean basin. Height and width measurements of types and available specimens are listed or plotted, and details are provided on protoconch, juvenile, and adult shell morphology. The photographs accompanying the descriptions are excellent, as is always the case with Jung's work, usually including three views of each selected specimen, and often scanning electron micrographs of the protoconch. Stratigraphic occurrences of all 13 taxa in the measured sections are illustrated, and referenced in the text to their locality numbers in the Naturhistorisches Museum Basel (NMB) and Tulane University (TU). Jung also includes comparisons with other Caribbean Recent and fossil species in his descriptions, where they are appropriate, and photographs of Recent specimens and types are provided. This particular feature makes the work itself all the more useful, by illustrating the author's reasoning regarding taxonomic similarities while allowing the reader to form his or her own opinions. Jung's philosophy regarding systematics is explained in his 1986 paper, which he references; due to the difficulty of identifying natural populations among fossils, any separable morphological groupings are considered separate species, even where it seems likely that they are conspecific.

My first impression, as a doctoral student researching columbellid systematics and evolutionary history, was that the generic placements of some of the species appeared incorrect. Also, the form identified as *Columbella* aff. *rus-*

ticoides actually looks much more similar to *C. submercatia*, with which it appears to be contemporaneous; size variation, which is the major difference between them, can be considerable within Recent species of *Columbella*. The form identified as *Nitidella* aff. *cibaica*, of which only one individual was collected, actually appears to be a species of *Columbella*, based on the presence of parietal denticles. It only serves as a reminder, however, that within the realm of traditional systematics, the notion of which characters are most important for a systematic diagnosis is up to the specialist. The characteristics necessary to identify a particular species or genus to one scientist may not be as significant to another. Until a robust phylogenetic hypothesis can be generated for the taxa in question, the systematic utility of any given character in those taxa cannot be objectively evaluated; and no such hypothesis yet exists for any portion of the Columbellidae. Given the quality of the information presented in this monograph, the research involved in generating those phylogenies will be much easier.

This monograph, and other issues of the *Bulletins of American Paleontology*, are available through the Paleontological Research Institution, 1259 Trumansburg Road, Ithaca, New York 14850.

Marta deMaintenon

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Architectonicidae of the Indo-Pacific (Mollusca, Gastropoda)

by RÜDIGER BIELER. 1993. *Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg*, vol. 30. Gustav Fi-

scher Verlag, Stuttgart. 377 pp., 286 figures. Priced by US distributors at \$100.00.

This is an excellent monograph of the heterobranch family Architectonicidae, or sundial shells, and far surpasses the last major review, Marshall's 1887 treatment in Tryon's *Manual of Conchology*. The author not only includes all the living species from the Indo-Pacific but also covers the taxa from the Eastern Pacific and discusses species from the Atlantic as well.

More than 22,000 specimens from over 50 museums worldwide have been examined. The author lists 250 species-level names, recognizes 88 species from 11 genera, and describes 20 new taxa. He uses as his principal morphological character the "finger print" pattern of spiral ribs on the post-larval shell. These profiles are diagrammatically represented in the text where they are often compared with those of similar species. Each species has been photographically figured from its three major aspects: apical, basal, and apertural; there are SEM views of protoconchs with their dimensions shown graphically, and maps which summarize locality data. Included are three color plates which compare shells, living animals in their habitats, and various stages of development. There is an introductory section which provides general information about the family and an extensive bibliography of almost 800 references which will be of use to any worker in Indo-Pacific malacology.

There are some issues which still remain to be resolved, including further studies using anatomical characters which may aid in resolving the phylogeny of the subfamilies, for which three clades are currently recognized. Treatment of the Atlantic taxa and coverage of the fossil species are also future projects. Despite these few loose ends, this is a major contribution to the study of marine gastropods and is highly recommended.

Henry Chaney

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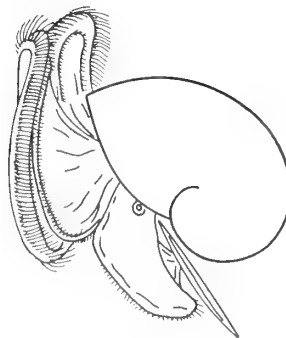
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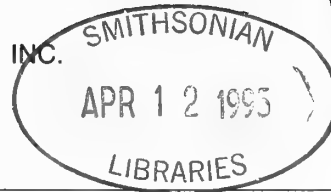
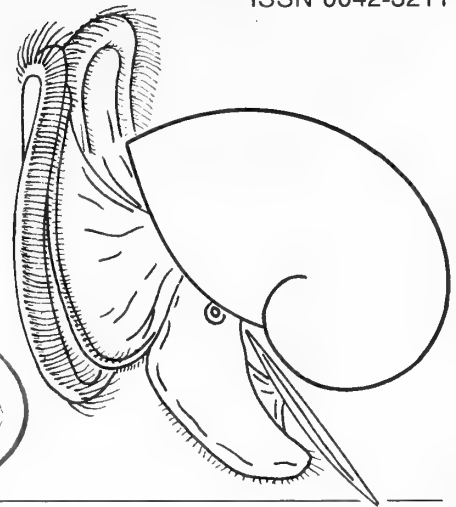
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THE VELIGER



A Quarterly published by
CALIFORNIA MALACOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 38

April 3, 1995

Number 2

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The Veliger (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

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Genetic Heterogeneity in Populations of *Littorina brevicula* (Philippi) (Mollusca: Gastropoda) in the Northern Part of Peter the Great Bay (Sea of Japan)

by

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Abstract. Genetic differences among eight samples of *Littorina brevicula* in Peter the Great Bay in the far east of Russia were surveyed using five highly polymorphic allozyme loci as genetic markers. Geographic distances between samples ranged from a few meters to more than a hundred kilometers. The coefficient of relative gene differentiation was quite low, $G_{ST} = 1.6\%$. Such a low level of differentiation was expected because *L. brevicula* has a planktonic larval stage lasting more than 10 days. Despite the low level of gene differentiation, there was statistically significant heterogeneity in allele frequencies among samples at three loci. Microgeographic heterogeneity (within a few dozen meters) among samples within continuous settlements was found to be significant in the loci *Pgi*, *Alpdh*, and *Fdh*. Differential natural selection, recruitment processes, and presence of a cryptic species are discussed as possible explanations for this observation.

INTRODUCTION

Most marine gastropod species have limited adult dispersal. One may expect that the level of gene flow among settlements of sedentary and poorly vagile species is largely determined by the mode of larval development (Scheltema, 1971). Species with a pelagic larval stage are characterized by a higher level of gene flow than those with a direct development (Ward, 1990). Undoubtedly, the extent of interpopulation differentiation should be related to the extent of gene flow if, at least, the genetic markers are neutral. However, it is interesting to evaluate to what extent the mode of larval development influences the level of genetic differentiation among populations.

Genetic-population structure has been described in a number of gastropod species both with a pelagic larval stage (Johnson & Black, 1982; Brown, 1991; Mitton et al., 1989; Campton et al., 1992) and with direct development (Grant & Utter, 1988; Day & Bayne, 1988; Day, 1990). Ward (1990) reviewed the biochemical genetics of *Littorina* species covering data for 10 species. The most

intensively studied species are *Littorina saxatilis* (Olivi, 1792), *L. arcana* Hannaford Ellis, 1978 (Ward & Warwick, 1980; Janson & Ward, 1984; Knight et al., 1987; Janson, 1987a, b; Knight & Ward, 1991), and *L. littorea* (Linnaeus, 1758) (Janson, 1987b; Johannesson, 1992). The level of interpopulation genetic differentiation in species with a direct development was shown to be higher than in species with planktonic larvae. For example, the average genetic differentiation among populations (expressed in G_{ST} and d_m) in seven littorinid species with pelagic larvae was about one-third that of the species with crawling young (Ward, 1990). However, the variation in, for example, G_{ST} , is large within both groups. Thus, despite a pelagic larval development, both *L. scutulata* Gould, 1849, and *L. plena* Gould, 1849, exhibit quite high levels of interpopulation genetic differentiation (Mastro et al., 1982; Ward, 1990).

Most studies describing genetic differentiation and population structure in littorinids have been done on Atlantic species. There have also been a few studies of genetic differentiation among populations of Pacific periwinkles

from the American coast (Mastro et al., 1982), but examples of western Pacific littorinids are absent.

The goal of this study was to measure the genetic differentiation among *Littorina brevicula* (Philippi, 1844) settlements in the northern part of Peter the Great Bay in the Sea of Japan, using polymorphic enzymes as genetic markers.

Littorina brevicula is one of the most common periwinkles in the Asian coast of the Pacific. This species ranges from Taiwan in the south to Peter the Great Bay in the north. Development of *L. brevicula* is entirely pelagic. Females produce pelagic egg capsules, from which planktonic larvae hatch in 8–10 days and the larvae remain in the plankton for some additional time (Golikov, 1976).

In this study, I have evaluated genetic heterogeneity among settlements of *L. brevicula* on different geographic scales, from meters to a hundred kilometers, using five enzyme loci which were earlier found to be highly polymorphic in this species (Tatarenkov, 1992).

MATERIALS AND METHODS

A total of 330 periwinkles were collected from eight locations in Peter the Great Bay in the Sea of Japan (Figure 1) in the summer of 1991. The first six samples (1–6) were collected in a small inlet in Vostok Bay. The distances between these samples ranged from two meters to 1 km. The other two samples (7, 8) were collected in Ussuriysky Bay, which is more than 100 km from Vostok Bay. The distance between 7 and 8 was about 100 m. Each sample was collected within 25 cm² of the shore. Snails were approximately of the same size, 7 to 10 mm. Individuals of this size are 3–4 years old.

The animals were kept alive in a cooler at 4°C prior to electrophoresis. The details of electrophoresis and of gel staining, and also of allozyme variation in *L. brevicula*, have been described earlier (Tatarenkov, 1992). Five polymorphic enzymes were chosen as genetic markers to investigate the level of interpopulation differentiation. These enzymes were: inorganic pyrophosphatase (E.C. 3.6.1.1, locus *Ipp*), alanopine dehydrogenase (E.C. 1.5.1.17, *Alpdh*), phosphoglucose isomerase (E.C. 5.3.1.9, *Pgi*), formaldehyde dehydrogenase (E.C. 1.2.1.1, *Fdh*), and peptidase (substrate gly-leu, E.C. 3.4.*.*., *Pep-2*). Loci coding for these enzymes was characterized by high heterozygosity levels, while zymogram patterns were easy to score. Allozymes of *Ipp*, *Pgi*, and *Fdh* were separated using Tris-EDTA-Borate buffer (pH 8.6), whereas Tris-Citrate (pH 7.0) was used for *Alpdh* and *Pep-2*.

Genotype frequencies of each sample were analyzed for consistency with Hardy-Weinberg expectations. The conventional chi-square test for goodness of fit between observed genotype distribution and those expected for random mating population would not be applicable to some of the samples because of small expected numbers of rare genotypes. Therefore, I estimated the significance of devia-

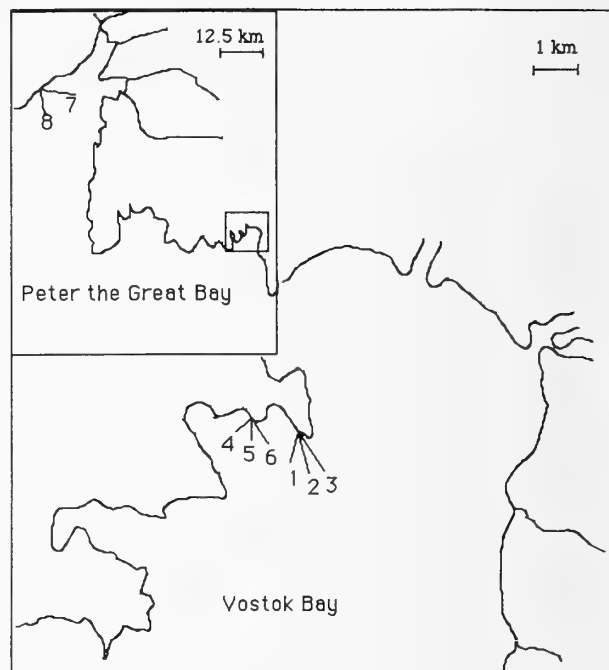


Figure 1

Locations of eight samples of *Littorina brevicula* in Peter the Great Bay. Samples 1–3 and 4–6 were collected in two continuous settlements of the species in Vostok Bay. Distances between the samples within the settlements ranged between two and 30 meters, while the distance between the settlements was about 1 km. Samples 7 and 8, with 100 meters in between, were from a continuous settlement in Ussuriysky Bay, which is about 100 km from Vostok Bay.

tions of observed genotype frequencies from those expected under Hardy-Weinberg equilibrium using a pseudo-probability test (Hernandez & Weir, 1989) provided by the program CHIRHW (Zaykin & Pudovkin, 1993). The program estimates the probability of the null hypothesis (agreement with Hardy-Weinberg equilibrium) using Monte-Carlo simulations.

Tests for homogeneity of allele frequencies among samples were performed with chi-square statistics. To avoid small expected numbers, I pooled the frequencies of the rarest alleles, so that expectations in contingency tables should not be less than 4, and tested for allele homogeneity with pooled frequencies. As an alternative approach, I estimated the hypothesis of allele frequency homogeneity using the pseudo-probability test (the CHIRXC program by Zaykin & Pudovkin, 1993). The combining of probabilities obtained with this test was performed using the Fisher's approach as given by Sokal & Rohlf (1981:779–782). This approach is based on the fact that natural logarithm of probability ($\ln P$) is distributed as $-0.5\chi^2_{[2]}$. Therefore, to evaluate the combined probability of null hypothesis, the $-2 \sum_i \ln P_i$ should be compared to χ^2 with

Table 1

Allele frequencies at five polymorphic loci in samples of *Littorina brevicula* from Peter the Great Bay (see Figure 1).

Locus	Allele	Sample							
		1	2	3	4	5	6	7	8
<i>Ipp</i>	(n)	50	40	18	45	46	45	45	41
	A	0.100	0.038	0.056	0.144	0.130	0.133	0.044	0.098
	B	0.850	0.863	0.889	0.767	0.815	0.767	0.900	0.817
	C	0.050	0.100	0.056	0.089	0.054	0.100	0.056	0.085
<i>Alpdh</i>	(n)	49	40	18	45	46	44	44	41
	A	0.041	0.063	0.000	0.044	0.076	0.125	0.114	0.024
	B	0.806	0.875	0.944	0.844	0.859	0.852	0.841	0.890
	C	0.082	0.038	0.056	0.044	0.011	0.023	0.045	0.024
<i>Pgi</i>	(n)	50	40	18	45	46	45	11	41
	A	0.080	0.013	0.000	0.022	0.011	0.011	0.000	0.000
	B	0.860	0.962	1.000	0.978	0.978	0.944	0.955	0.988
	C	0.060	0.025	0.000	0.000	0.011	0.044	0.045	0.012
<i>Fdh</i>	(n)	39	40	18	45	46	45	45	41
	A	0.103	0.112	0.056	0.089	0.087	0.044	0.133	0.146
	B	0.064	0.013	0.139	0.067	0.043	0.111	0.000	0.073
	C	0.833	0.875	0.806	0.844	0.870	0.844	0.867	0.780
<i>Pep-2</i>	(n)	15	40	17	43	46	45	44	41
	A	0.033	0.013	0.029	0.023	0.022	0.011	0.023	0.037
	B	0.433	0.363	0.412	0.337	0.478	0.389	0.341	0.463
	C	0.367	0.575	0.529	0.581	0.478	0.544	0.580	0.488
	D	0.167	0.050	0.029	0.058	0.022	0.056	0.057	0.012

2k degrees of freedom (k = the number of separate tests and probabilities).

When testing for conformity of genotype distribution to Hardy-Weinberg equilibrium or testing for homogeneity of allele frequencies among samples, one usually has to perform a number of separate tests (for individual loci and for different sets of samples). In such cases of multiple testing, the critical values of coefficients of significance for each individual test are not equal to the value in a single test. Indeed, according to statistical expectations, approximately five out of 100 tests performed are expected to result in P -values less than 0.05 by chance only. To avoid type I errors, I performed corrections for multiple tests using Sidak's multiplicative inequality for calculations of critical values of chi-square distribution (Sokal & Rohlf, 1981:728; Rohlf & Sokal, 1981:101). I used the program MULTTEST (Zaykin & Pudovkin, 1991) to find the critical values of χ^2 for each individual (replicate) test considering that it was a part of a group of analogous and independent tests.

The relative amount of genetic variation among populations was analyzed using Nei's (1973) measure of gene diversity, G_{ST} .

RESULTS

Allele frequencies with corresponding sample sizes for the five loci studied are given in Table 1. At *Ipp* the observed

genotype ratios did not differ significantly from Hardy-Weinberg expected ratios. At the remaining four loci, significant deviations (pseudo-probability test, $P < 0.005$) were present in one or two samples. After correction for multiple testing for each locus separately, the deviations were still significant. When considering all five loci and eight samples and applying the corresponding Sidak correction for the whole set of tests, the deviations from Hardy-Weinberg expectations were significant in samples 1 and 2 for *Pgi* ($P < 0.05$), and in sample 5 for *Alpdh* ($P < 0.05$). These deviations were due to a deficiency of heterozygotes.

Statistically significant allele frequency heterogeneity among the eight samples of *L. brevicula* was present in *Alpdh*, *Pgi*, and *Fdh* (Table 2). Considering, however, these tests as a set of multiple tests and applying Sidak's correction, the heterogeneities in *Alpdh* and *Fdh* can be explained by a statistical type I error. However, heterogeneity in *Pgi* remained significant ($0.01 < P < 0.05$). The combined test for heterogeneity over all loci revealed significant differences among samples ($P < 0.001$); even disregarding data on *Pgi*, the combined probability over the four remaining loci was also significant ($P < 0.05$).

Samples 1-3, 4-6, and 7, 8 were collected in three different settlements. Within each settlement, the spatial distribution of mollusks was continuous. Settlements were disrupted by places where *L. brevicula* was not present (e.g., sand beaches). Within the settlements, samples were

Table 2

Conventional χ^2 -test and pseudo-probability test for heterogeneity in allele frequencies of five polymorphic loci among eight samples of *Littorina brevicula*. Numbers of alleles, χ^2 -values, and degrees of freedom are referred to χ^2 -test. P and P_{pseudo} -probabilities of null hypothesis obtained with χ^2 -test and with pseudo-probability test, respectively.

Locus	Num- ber of al- leles*	χ^2	d.f.*	P	P_{pseudo}
<i>Ipp</i>	3	16.04	14	0.311	0.301
<i>Alpdh</i>	3	28.50	14	0.012	0.012
<i>Pgi</i>	2	26.00	7	0.0005	0.005
<i>Fdh</i>	3	24.75	14	0.037	0.038
<i>Pep-2</i>	3	16.73	14	0.271	0.360
Total		112.02	63	0.0001	0.0007

* Rare alleles were pooled so that expected numbers should not be less than 4.

taken at distances of between two meters (samples 2 and 3) to 100 meters (samples 7 and 8). It is likely, that, within the settlements, gene exchange may be due to movements of adult snails, in addition to exchange through pelagic larvae. The results of pseudo-probability tests for heterogeneity of samples within continuous settlements are shown in Table 3. Statistically significant heterogeneity of allele frequencies was found between samples 1-3 in *Pgi*, and between 7 and 8 in *Alpdh* and *Fdh*. Combining the probabilities over all three settlements, I concluded that samples within continuous settlements were significantly different in *Alpdh* ($P < 0.005$), *Pgi* ($P < 0.05$), and *Fdh* ($P < 0.05$). The totals over five loci for each settlement were significant for samples 1-3 ($P = 0.018$), and 7, 8 ($P = 0.002$). The combined probability over all loci and all groups of samples shows that samples within continuous settlements do differ in allele distributions ($P < 0.001$).

Table 4 outlines estimates of gene diversity among *L. brevicula* samples. The average coefficient of gene differentiation is quite low, G_{ST} being 1.6% only. Thus, almost all variation observed is explained by within sample component. However, at *Pgi* the between sample component of gene diversity is somewhat larger, $G_{ST} = 3.7\%$.

Considering the five polymorphic loci of this study, Nei's (1972) index of gene identity (I) ranged from 0.9860 between samples 1 and 4 to 0.9987 between 2 and 7, with an average of 0.9926.

DISCUSSION

Despite dozens of papers devoted to genetic-population structure in littorinids, data on Hardy-Weinberg equilibrium are quite poor. As Ward (1990) noted, this may be because most *Littorina* species show Hardy-Weinberg proportions. This is in contrast to the situation in bivalve

Table 3

Pseudo-probability test for heterogeneity among samples within continuous settlements of *Littorina brevicula*-test for microgeographic variation. P_{pseudo} -probability of null hypothesis that allele frequencies among samples do not differ.

Locus	Samples			Total
	1-3	4-6	7, 8	
<i>Ipp</i>	P_{pseudo} 0.359	P_{pseudo} 0.818	P_{pseudo} 0.313	P_{pseudo} 0.569
<i>Alpdh</i>	0.211	0.082	0.003	0.003
<i>Pgi</i>	0.017	0.198	0.363	0.037
<i>Fdh</i>	0.075	0.343	0.015	0.015
<i>Pep-2</i>	0.231	0.535	0.169	0.258
Total	0.018	0.283	0.002	0.0008

mollusks in which many cases of deviations from Hardy-Weinberg equilibrium have been described (reviewed by Zouros & Foltz, 1984). Different kinds of selection models, assortative mating, Wahlund effects, and null-alleles have been suggested as explanations for these.

The majority of samples of *L. brevicula* were in good agreement with Hardy-Weinberg proportions at most loci. There was no general tendency for deficit or excess of heterozygotes as well. However, there were a few significant cases of departures from Hardy-Weinberg expectations in *Pgi* and *Alpdh*. It seems unlikely that the heterozygote deficiencies in *Pgi* or *Alpdh* of *L. brevicula* populations were caused by the presence of null-allele because I did not observe even a single case of no-enzyme activity on zymograms. Assuming that the deviations found in *Pgi* were due to a null-allele, the frequency of this allele should have been about 0.25, and a total of 19 null-allele homozygotes should have been expected in my data as blank tracks on the zymograms. As Richardson et al. (1986) pointed out, null-allele homozygotes may not be present if they are lethal or have a reduced fitness. It is doubtful, however, that such deleterious alleles could exist in population at such a high frequency of 0.25.

The Wahlund effect seems also to be an unlikely explanation for the heterozygote deficiency. Differences in allele frequencies among demes must be very large in this case to explain the heterozygote deficiency found. In fact, the variance of allele frequencies among the samples of this study may explain only about 3% of the mean heterozygote deficiency found in *Pgi*, and less than 1% of the deficiency in sample 1. However, as this study includes geographic variation in allele frequencies over a minor area of the species total distribution, a Wahlund effect may be caused by larval input from remote populations which could have substantially different allele frequencies. If this is the case, however, such larval influx from other areas must be very rare. Otherwise, it would be difficult to explain the required high geographical variation in allele

frequencies over the species area. Occasional influx of larvae from remote areas is known in the literature. Johannesson (1992) described a case of a mass occurrence of *Melarhappe neritoides* (Linnaeus, 1758) in Sweden, where this species has previously been absent. However, no cases of substantial geographic variation in gastropods with planktonic larvae have been described. Instead, similarities of allele frequencies over vast areas have been described for littorinids *L. littorea* and *Melarhappe neritoides* (Johannesson, 1992), the conch *Strombus gigas* Linnaeus (Mitton et al., 1989; Campton et al., 1992), the abalone *Haliotis rubra* (Brown, 1991), and an undescribed species of limpet of the genus *Siphonaria* Sowerby, 1823 (Johnson & Black, 1982). There are no reasons to believe that *L. brevicula* is an exception to these cases.

Assortative mating seems to be an unlikely explanation in relation to electrophoretic characters, unless these are tightly linked to a locus controlling visible characteristics, and in linkage disequilibrium with it (Richardson et al., 1986).

Of the remaining models which may explain the observed deviations from Hardy-Weinberg equilibrium, natural selection against heterozygotes or the presence of a reproductively isolated taxon, which I may have included by mistake together with *L. brevicula*, seem to be likely ones. However, without additional data, it is difficult to choose between these two hypotheses.

If the investigator is certain that he is dealing with only one taxon, microgeographic heterogeneity of allele frequencies in a species with a high level of gene flow may be substantial evidence for local natural selection. An example of variation due to selection at several loci on a small scale (dozens of meters) was found in the bivalve mollusk *Crenomytilus grayanus* (Dunker) with pelagic larvae (Pudovkin & Balakirev, 1985). Other examples of supposed selection based variation on microgeographic scale are in the limpet snail *Siphonaria* sp. (Johnson & Black, 1982) and in the copepod *Tigriopus californicus* (Baker, 1912) (Burton & Feldman, 1981). Assuming that *L. brevicula* is a taxonomically uniform group, the significant heterogeneity in allele frequencies among samples within some dozen meters that was found in *L. brevicula* is unexpected because the larvae of this species spend at least 10 days in plankton. Therefore, one might expect a reasonable shuffle of genes during that period within the bay plankton. Besides, there is an exchange of genes due to migration of adult snails in continuous settlements. Therefore, the microgeographic variation found could not be explained by stochastic drift of allele frequencies. The heterogeneity of allele frequencies among samples within continuous settlements, and also among settlements within an inlet, may be caused by differential natural selection. It is not necessary that this selection act directly on the allozyme loci. It might be selection on a closely linked locus or loci.

The other possible reasons might be the presence of unknown isolated taxon or genotype-dependent distribution of individuals along the shore. The latter explanation

Table 4

Analysis of gene diversity (Nei, 1973) based on five polymorphic loci for eight samples of *Littorina brevicula*.

Locus	H _T	H _S	G _{SL}	G _{LT}	G _{ST}
<i>Ipp</i>	0.2903	0.2871	0.0055	0.0055	0.0110
<i>Alpdh</i>	0.2740	0.2426	0.0142	0.0036	0.0178
<i>Pgi</i>	0.0813	0.0783	0.0221	0.0148	0.0369
<i>Fdh</i>	0.2811	0.2774	0.0085	0.0046	0.0132
<i>Pep-2</i>	0.5664	0.5571	0.0157	0.0007	0.0164
Average	0.2932	0.2885	0.0123	0.0038	0.0161

H_T = total heterozygosity.

H_S = mean sample heterozygosity.

G_{SL} = relative gene differentiation among samples within continuous settlements.

G_{LT} = relative gene differentiation between continuous settlements.

G_{ST} = relative gene differentiation among samples.

seems unlikely, as we deal with variation at allozyme loci. Until now very few examples of association between enzyme polymorphism and habitat selection behavior have been known (Byers, 1983). Furthermore, it is possible to give other explanations of association of enzyme polymorphism with habitat types instead of genotype-dependent habitat choice. Thus, in the case with *Tegula funebris* (A. Adams, 1855) (Byers, 1983), it might be selection in favor of certain alleles at *Pgi* and *Pgm*, which is coupled with different habitat preferences of shore levels by individuals of different ages.

The possibility of the presence of a taxon morphologically similar to *L. brevicula* is difficult to reject. In Peter the Great Bay, some forms of *L. mandshurica* Schrenck, 1867, have shell morphology similar to *L. brevicula*. However, these species are distinct in drastic differences in *Pep-2*, *Alpdh*, and *Fdh*, which in combination make it impossible to mistake *L. mandshurica* for *L. brevicula*. However, it might be another taxon, which is at present unknown. I should stress here, that this presumed taxon must be genetically very close to *L. brevicula*, as it has the same alleles at five polymorphic loci. Furthermore, I did not observe any indication for the presence of reproductively isolated taxon when I previously explored *L. brevicula* for 39 loci (Tatarenkov, 1992). Still, the hypothesis of presence of unknown taxon deserves further investigation. Recently Takada (1992) discovered that in southern Japan in early winter, before copulation occurs, some snails of *Littorina brevicula* migrate down the shore as far as 20 meters, whereas the other snails remain in the upper intertidal zone. In early spring, presumably after copulation and releasing of veligers, snails begin to move upward again. In summer the distribution of individuals is unimodal. Later Takada put forward a hypothesis of the presence of two different species (personal communication). However, it is not yet known if this migration causes some kind of reproductive isolation. It is necessary to show that the very

same snails and their descendants show such migration, and that this does prevent gene flow between the two groups. Besides, it is not yet known if such partition of population is characteristic for the snails from Peter the Great Bay. Thus, in northern Japan not some but all adult snails showed downward migration in winter (Kojima, 1957, 1959). Summarizing, however, it is necessary to say that there might be some unknown peculiarities of biology leading to some kind of assortative mating and reproductive isolation, which might explain microgeographic heterogeneity in *L. brevicula*.

Despite the statistically significant heterogeneity in allele frequencies at some polymorphic loci, *L. brevicula* is characterized with low genetic differentiation in general. Thus, the average coefficient of gene differentiation (G_{ST}) in the species is only 1.6%. This is comparable to the value of 1–2% obtained for *L. littorea* which also has a pelagic larval stage (Janson, 1987b). In contrast, the differentiation among populations of ovoviviparous *Littorina saxatilis* over similar geographic scales ranges from 7 to 12% (Janson, 1987b; Ward & Warwick, 1980). In the likewise direct developing species *Littorina arcana* and *L. nigrolineata* Gray, 1839, although on a somewhat larger geographic scale, G_{ST} is in the range of 16% to 18% (Knight et al., 1987; Knight & Ward, 1991). This indicates that gene flow through planktonic dispersal in *L. brevicula* largely prevents the accumulation of genetic divergence (which may occur due to both genetic drift and differential selection).

The data of this paper demonstrate that investigation of microgeographic genetic-population structure of mollusks with planktonic dispersal poses many interesting questions. Usually species with pelagic larvae show little or no differentiation among populations over broad areas. However, sometimes this similarity of allele frequencies over broad areas is accompanied by patchy microgeographic variation. There is no universal explanation for such heterogeneity at present. Three main explanations for such patchiness are possible:

(1) Local natural selection. The cases of microgeographic variation in species with planktonic dispersal can be explained by natural selection, because the role of genetic drift in local settlements becomes negligible as a consequence of extensive gene exchange. The more substantial evidences of natural selection might be the cases of repeated correlations of certain environmental factors with allozyme variation. However, the probability of observing such cases is rare because one can study only a limited number of both environmental parameters and polymorphic loci.

(2) Presence of a cryptic taxon. It is always possible to assume that material at study is taxonomically heterogeneous. If a large number of loci were surveyed and no diagnostic loci were found, presence of a cryptic taxon becomes less likely, but still difficult to reject completely.

(3) Unknown peculiarities of larval dispersal. The assumption of widespread gene flow might be misleading. Discrete cohorts of larvae are possibly maintained due to

the complex nature of sea currents or unknown peculiarities of larval behavior.

Further observations should be performed to choose between the hypotheses explaining microgeographic heterogeneity in *L. brevicula*.

ACKNOWLEDGMENTS

I am grateful to Dr. A. I. Pudovkin for the discussions, and to Dr. K. Johannesson for the valuable suggestions and comments on the manuscript. Dr. Thierry Backeljau and an anonymous reviewer provided helpful criticism and advice. This work was supported in part by grants from the Russian Governmental Scientific and Technical Project "Priority Directions of Genetics Development," and from the Youth Foundation (Russia, Novosibirsk). Financial assistance by the George Soros Scholarship from the International Science Foundation is thankfully appreciated.

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Recent and Tertiary Trochaclididae from the Southwest Pacific (Mollusca: Gastropoda: Trochoidea)

by

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Abstract. Twenty-three species of the Trochaclididae (15 new species) are recorded, 17 from the New Zealand region, five from Australia, and one from New Caledonia. These taxa are referred to *Trochaclis* Thiele, 1912 (Early Miocene–Recent), *Acremodonta* Marshall, 1983 (Recent), *Acremodontina* gen. nov. (Early Miocene–Recent), and *Austrotrochaclis* gen. nov. (Recent). Trochaclidid radulae with central and lateral teeth that are strongly differentiated from the marginal teeth are recorded for the first time.

INTRODUCTION

The Trochaclididae are a group of marine gastropods with small, rather undistinguished shells, yet with radular teeth that are extremely distinctive in having repeatedly divided tips. Most of the few species that have been taken alive were living in cavities of glass sponges (Porifera: Hexactinellida) or occurred loose in dredge samples that included these sponges or abundant spicules (Warén, 1989; Hain, 1990; Hickman & McLean, 1990; personal observation). Gut contents indicate spongivory (S. Hain in Warén, 1992; personal observation).

Trochaclis antarctica Thiele, 1912 was the only trochaclidid known until recently, when *T. islandica* Warén, 1989, and *T. versiliensis* Warén, Carrozza & Rocchini, 1992, were named, based on North Atlantic and Mediterranean material. Two undescribed species were recorded from the north-eastern Pacific by Hickman & McLean (1990). The New Zealand species *Acremodonta crassicosta* (Powell, 1937) has also proved to be a trochaclidid. In the present contribution I introduce a further 22 species, of which 15 are new and seven are transferred from the other families.

Abbreviations and Text Conventions: AMS—Australian Museum, Sydney; BMNH—The Natural History Museum, London; LACM—Los Angeles County Museum of Natural History; MNHN—Muséum National d'Histoire Naturelle, Paris; MV—Museum of Victoria, Melbourne; NMNZ—Museum of New Zealand, Wellington; NZGS—Institute of Geological and Nuclear Sciences, Lower Hutt; NZOI—National Institute of Water

and Atmospheric Research, Wellington. In references to dimensions height precedes diameter.

SYSTEMATICS

Order Archaeogastropoda Thiele, 1925

Suborder Vetigastropoda Salvini-Plawen, 1980

Superfamily TROCHOIDEA Rafinesque, 1815

Family TROCHACLIDIDAE Thiele, 1929

Trochaclididae Thiele, 1929:179.

Trochaclisidae Wenz, 1939:650 (incorrect spelling variant).

Acremodontinae Marshall, 1983:127.

Diagnosis: Shell turbiniform, 1.30–ca. 9 mm in maximum dimension. Marginal teeth very slender, tips repeatedly divided. Central and lateral teeth short and scalelike (*Acremodontina*), or similar to marginals (*Trochaclis*, *Acremodonta*). Edge of oral disc (*Acremodonta*) set with dendritic papillae, operculum chitinous.

Remarks: *Trochaclis* Thiele, 1912 was originally referred to Ptenoglossa by Thiele (1912) because the radula seemed to him to resemble that in *Aclis* Lovén (Janthinoidea, Aclididae). Thiele (1929) later grouped his new family Trochaclididae *incertae sedis* among the lower Mesogastropoda (i.e., Caenogastropoda) where it long resided (Wenz, 1939; Boss, 1982; Vaught, 1989). Recently Warén (1989) illustrated the radula of *Trochaclis* for the first time and showed that it differs from those of Ptenoglossa in various details,

including the presence of repeatedly divided tips. He referred the family to Archaeogastropoda because the shell morphology and Thiele's (1912, 1929) description of the animal were not discordant with this interpretation. The presence of a well-developed nacreous layer in *Acremodonta* Marshall, 1983, and of a thin scattering of platelets (probably a vestigial nacreous layer) on the inner shell surface of all of the other species discussed below (personal observation), and of short multiple lateral radular teeth in some of them, are strong support evidence for a position in Trochoidea.

When introducing Acremodontinae (Marshall, 1983), I was misled by Thiele's misinterpretation of the radular morphology of *Trochaclis*, which is in fact fundamentally similar to that in *Acremodonta* Marshall, 1983, the type genus. The type species of *Acremodonta* and *Trochaclis* have respectively strong spirally sculptured and essentially smooth teleoconchs, whereas the radular teeth in *Acremodonta* are much more slender. Despite these differences, the genera are evidently confamilial because some of the species described below have intermediate shell and radular morphologies.

In this contribution I introduce a new genus (*Acremodontina*) in which the central and lateral teeth are short, scalelike and morphologically strongly differentiated from the slender marginal teeth, which exhibit the terminal branching characteristic of the family (Figure 68). This hitherto unknown radular plan differs markedly from that in *Trochaclis* (Warén, 1992:figs. 37A, 37B, 38A, 38B) and *Acremodonta* (Marshall, 1983:figs. 2A–E), in which the teeth in the central field, though shorter than the outer marginals, grade insensibly with the inner marginals. The central and lateral teeth in *Acremodontina* resemble those of Umboniinae (Trochidae—Hickman & McLean, 1990) and *Dillwynella* Dall, 1889 (Skeneidae?—Marshall, 1988). Assuming that the outer lateral teeth in Trochaclididae arise through progressive morphological transformation of inner marginal teeth as in Trochoidea (other than *Callostoma* Swainson, 1840) (Warén, 1990), it would seem that the degree of transformation is strongest in *Acremodontina* and totally retarded in *Acremodonta*, in which all of the teeth in the central field are morphologically marginals. The adult radula in *Trochaclis* exhibits an intermediate state of transformation in that the central tooth and positionally lateral teeth are relatively shorter and broader than the outer marginals, though longer and narrower than in *Acremodontina*. Since all of the teeth in the *Acremodonta* radula are relatively by far the longest and narrowest of any trochaclidid, and are also exceptionally slender for a trochoidean, this is evidently a derived state (apomorphic). Whether or not the wide central and lateral teeth in *Acremodontina* are physically involved in food processing, they may be a developmental legacy from a source group that had a different diet and feeding mode. Whatever the case, they are probably a developmentally economical means of enhancing width of the marginal

fields, which has been achieved in *Acremodonta* by extreme elongation of all of the teeth.

Hickman & McLean (1990) ranked Trochaclidinae as a subfamily of uncertain affinity in Trochidae. As these authors admitted, the radula and oral disc papillae are highly distinctive, and, in my opinion, the group is worthy of familial status within Trochoidea. While Trochaclididae almost certainly belongs in Trochoidea, its relationships within the superfamily are obscure. The marginal tooth morphology is so distinctive that it does not suggest a sister-group relationship with any other specific taxon of Trochoidea. Trochaclidid marginal tooth morphology, especially in *Acremodontina* is strongly convergent with that in *Perotrochus* Fischer, 1885 (Vetigastropoda, Pleurotomariidae) and *Seila* A. Adams, 1861 (Caenogastropoda, Cerithiopsidae) (Hickman, 1984:figs. 10, 17), which are also spongivores (compare with Figures 62, 69, 72).

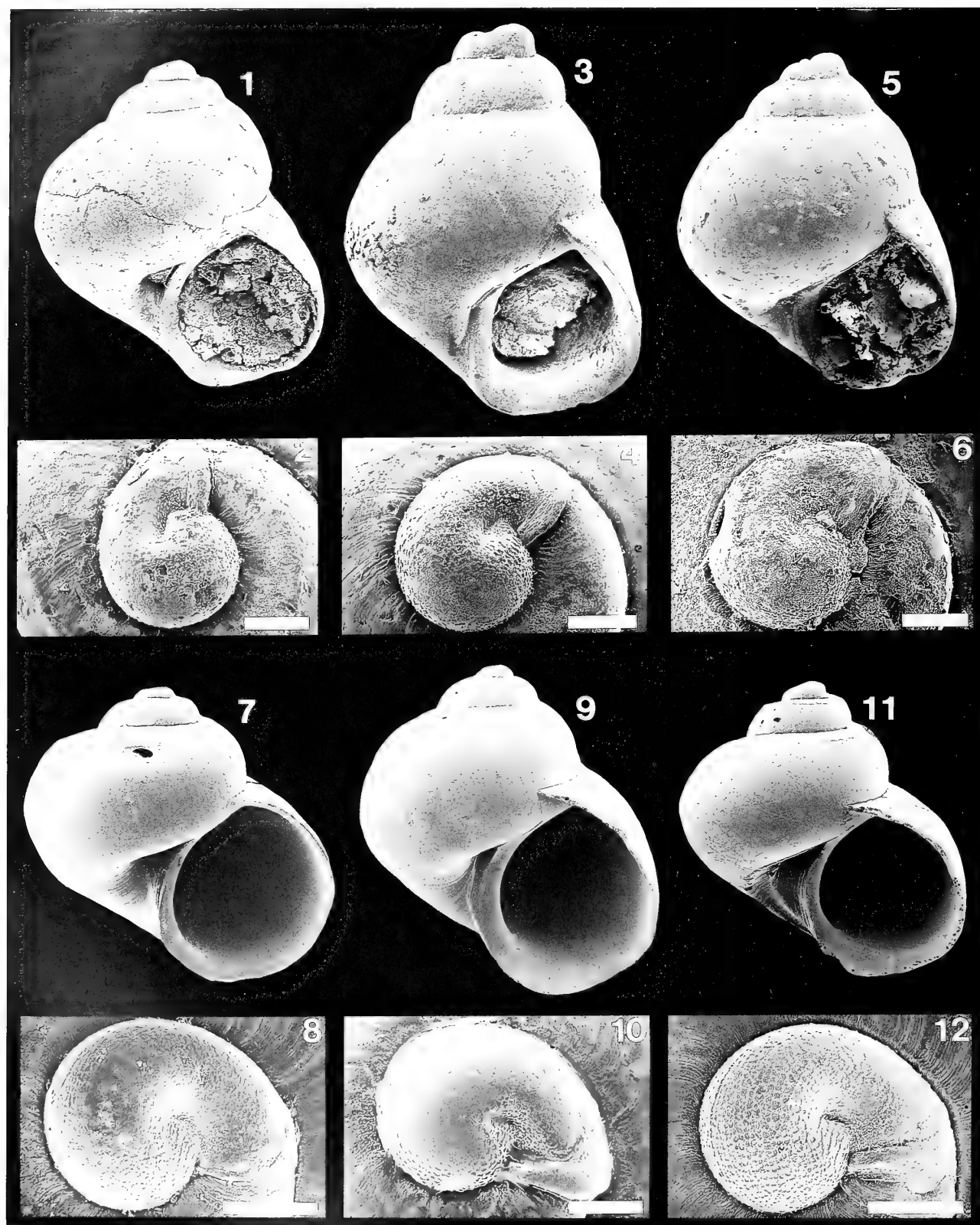
Genus *Trochaclis* Thiele, 1912

Trochaclis Thiele, 1912:192 Type species (by monotypy):
Trochaclis antarctica Thiele, 1912; Recent, Antarctica.

Diagnosis: Shell turbiniform, up to about 2.00 mm wide, narrowly umbilicate or anomphalous, white. Interior surface set with scattered platelets, presumably aragonite, and representing vestigial nacreous layer. Protoconch of less than one whorl, sculptured with fine network of crisp threads that enclose irregularly polygonal spaces, tip of apical fold pinched. Teleoconch whorls convex, a rounded varix early on first whorl, with or without shoulder angulation on first one or two whorls or (one species) with shoulder and peripheral keel on all whorls, with or without few basal spiral threads. Radular formula $\infty + 1 + \infty$. Central tooth slender, with fine terminal cusps. Lateral(s) and marginals slender, morphologically intergrading, narrowing outward, each with long series of fine cusps, cusps at tips repeatedly divided. Operculum chitinous, multispiral. Animal (Thiele, 1912): eyes on processes at bases of cephalic tentacles, ctenidium consisting of few lamellae, osphradium a narrow, longitudinal fold, no salivary gland, esophagus with a glandular swelling; cerebral ganglia united, connected with pedal ganglia via long commissures.

Remarks: Although Warén (1992) considered that *Trochaclis* species lack a central tooth, it seems likely that this tooth is in fact shown in one of his illustrations of the radula of *T. antarctica* (Warén, 1992:fig. 37A, tooth at exact center). If so, the central tooth in *Trochaclis* is similar to the lateral teeth, which in turn grade insensibly into the marginal teeth.

None of the *Trochaclis* species described below has been collected alive; they are referred to this genus because of the extreme similarity of the shells to those of species for which the radula is known. Shells of typical *Trochaclis* species are distinctive in combining a finely reticulate protoconch, a varix shortly after the protoconch, and subse-



quent whorls that are smooth apart from (usually) a shoulder spiral on first one or two whorls, and one or more spiral threads beside umbilical area. Of the numerous skeinimorph genera with superficially similar type species, the one they are most likely to be confused with is *Moelleriopsis* Bush, 1897 (type species *M. abyssicola* Bush, 1897), the protoconch of which, however, is spirally lirate, whereas the radula is entirely different (see Warén, 1992).

Trochaclis bucina (Laws, 1941)

(Figures 3, 4; Table 1)

Notosetia bucina Laws, 1941:141, fig. 31.

"*Notosetia*" *bucina*. Fleming, 1966:44.

Powellisetia (?) *bucina*. Beu & Maxwell, 1990:405.

Description: Shell turbiniform, up to 2.12 mm high, higher than wide, spire up to $0.86\times$ as high as aperture, of moderate thickness, anomphalous, glossy.

Protoconch 300 μm wide, tip of apical fold pinched, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.75 convex whorls; a strong rounded varix immediately after protoconch, first whorl strongly convex, subsequent whorls more weakly convex, periphery rounded, base almost flat. Smooth apart from fine, crowded collabral growth lines. Aperture subcircular, peristome strongly discontinuous; outer lip thin at rim, thicker within; parietal glaze of moderate thickness; inner lip thick, especially abapically.

Type data: Holotype NZGS TM 1275, Pakaurangi Point, Kaipara Harbour; Otaian (Early Miocene).

Other material examined: (9 specimens). Pakaurangi Point, Kaipara Harbour, C. R. Laws (2 paratypes of *Dolicrossea atypica* Laws); GS 9730, tuffaceous siltstone, small bay ca. 1.6 km NW of Pakaurangi Point, map ref. Q8/262513 (f9828), March, 1979, B. A. Marshall and P. A. Maxwell (2 NMNZ, 5 NZGS)—Otaian (Early Miocene).

Table 1

Trochaclis bucina (Laws, 1941). Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.15	0.93	1.24	2.30	GS 9730
1.35	1.03	1.31	2.60	GS 9730
1.40	1.10	1.27	2.60	GS 9730
1.40	1.10	1.27	2.70	GS 9730
1.40	1.13	1.24	2.60	GS 9730
<i>1.50</i>	<i>1.10</i>	<i>1.36</i>	<i>2.75</i>	<i>GS 9730</i>
2.12	1.75	1.21	3.30	GS 9730

Distribution: Early Miocene (Otaian), Pakaurangi Point, Kaipara Harbour, northern New Zealand.

Remarks: Among previously described *Trochaclis* species, *T. bucina* is distinctive in having a tall, narrow spire. Two similar Recent species are described below.

Two of the specimens examined are paratypes of *Dolicrossea* (i.e., *Trochaclis*) *atypica* from the C. R. Laws collection (NZGS).

Although superficially similar to the type species of *Notozetia* Iredale, 1915, the type species of that genus (*Cirsonella neozelanica* Murdoch, 1899) has a smooth protoconch and lacks a varix on the first teleoconch whorl, while the radular teeth are not dentritically branched (personal observation).

Trochaclis atypica (Laws, 1939)

(Figures 1, 2; Table 2)

Dolicrossea atypica Laws, 1939:480, fig. 61.

(?) *Dolicrossea atypica*. Fleming, 1966:41, Beu & Maxwell, 1990:403.

Description: Shell turbiniform, up to 1.55 mm high, slightly higher than wide at maturity, spire $0.65\text{--}0.83\times$ as high as aperture, of moderate thickness, glossy, with small, narrow umbilical chink.

Explanation of Figures 1 to 12

Figures 1–12. *Trochaclis* species. Scales 100 μm .

Figures 1, 2. *Trochaclis atypica* (Laws, 1939), topotype (NZGS TM 7681), Early Miocene, Pakaurangi Point, Kaipara Harbour, New Zealand, shell height 1.40 mm.

Figures 3, 4. *Trochaclis bucina* (Laws, 1941), topotype (NZGS TM 7680), Early Miocene, Pakaurangi Point, Kaipara Harbour, New Zealand, shell height 1.35 mm.

Figures 5, 6. *Trochaclis kaiparica* Marshall, sp. nov., holotype, Early Miocene, Pakaurangi Point, Kaipara Harbour, New Zealand, shell height 1.70 mm.

Figures 7, 8. *Trochaclis morningtonensis* Marshall, sp. nov., holotype, Late Miocene, Fossil Beach, Port Phillip, Victoria, Australia, shell height 1.75 mm.

Figures 9, 10. *Trochaclis calva* Marshall, sp. nov., holotype, off Three Kings Islands, northern New Zealand, 805 m, shell height 1.95 mm.

Figures 11, 12. *Trochaclis regalis* Marshall, sp. nov. Figure 11. Holotype, off Three Kings Islands, northern New Zealand, 710 m, shell height 1.58 mm. Figure 12. Paratype (NMNZ M.117511), off Three Kings Islands, 310 m.

Table 2

Trochaclis atypica (Laws, 1939). Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.20	1.20	1.00	2.20	GS 9730
1.25	1.20	1.04	2.30	GS 9730
1.30	1.25	1.04	2.40	GS 9730
1.32	1.23	1.07	2.40	GS 9730
1.40	1.23	1.14	2.50	GS 9730
1.40	1.30	1.07	2.60	GS 9730
1.40	1.30	1.07	2.50	GS 9730
1.45	1.28	1.13	2.50	GS 9730
1.55	1.42	1.09	2.70	GS 9730

Protoconch 280–300 μ m wide, tip of apical fold pinched, a distinct angulation on last quarter whorl, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.70 convex whorls, a strong rounded varix immediately after protoconch, periphery rounded, base almost flat, most of first whorl with pronounced shoulder angulation. Smooth apart from fine, crowded collabral growth lines. A narrow angulate spiral thread descending steeply from umbilical chink and coalescing with apertural rim. Aperture subcircular, outer lip thin at rim, thicker within; parietal lip rather thin; inner lip thick, especially abapically.

Type data: Holotype NZGS TM 1311: Pakaurangi Point, Kaipara Harbour; Otaian (Early Miocene).

Other material examined: (12 topotypes). GS 9730, tuffaceous siltstone, small bay ca. 1.6 km NW of Pakaurangi Point, map of ref. Q8/262513 (f9829), March 1979, B. A. Marshall and P. A. Maxwell—Otaian, (Early Miocene) (4 NMNZ, 8 NZGS).

Distribution: Early Miocene (Otaian), Pakaurangi Point, Kaipara Harbour, northern New Zealand.

Remarks: *Trochaclis atypica* is characterized by its low spire, angulate protoconch and first teleoconch whorl, narrow umbilical chink, and lack of basal spiral cords. The protoconch angulation is a particularly distinctive feature. As noted above, the two paratypes represent *T. bucina*.

Species of *Dolicrosssea* Iredale, 1924, with which *T. atypica* was formerly associated, differ in having a spirally lirate teleoconch, a strong swelling outside the umbilicus, a sinuous apertural profile, and in other details.

Trochaclis kaiparica Marshall, sp. nov.

(Figures 5, 6)

Description: Shell turbiniform, up to 1.72 mm high, higher than wide at maturity, spire 0.85 \times as high as aperture, of moderate thickness, glossy, with tiny umbilical chink.

Protoconch 300–330 μ m wide, tip of apical fold pinched, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.75 convex whorls, a strong rounded varix immediately after protoconch, first whorl strongly convex, subsequent whorls more weakly convex, periphery rounded, base almost flat, tightly rounded into umbilical chink. Smooth apart from fine, crowded collabral growth lines. Aperture subcircular; outer lip thin at rim, thicker within; parietal glaze of moderate thickness; inner lip thick, especially abapically.

Type data: Holotype TM 7667 (1.70 \times 1.53 mm, 2.75 teleoconch whorls) and immature paratype NZGS: GS 9730 tuffaceous siltstone, small bay ca. 1.6 km NW of Pakaurangi Point, Kaipara Harbour, map ref. Q8/262513 (f9828), March 1979, B. A. Marshall and P. A. Maxwell; Otaian (Early Miocene).

Distribution: Early Miocene (Otaian), Pakaurangi Point, Kaipara Harbour, northern New Zealand.

Remarks: *Trochaclis kaiparica* occurs in the same beds as *T. bucina* and *T. atypica*, differing from the former in having a more broadly angulate spire, and from the latter in lacking angulations on the protoconch and first teleoconch whorl and in being anomphalous.

Etymology: From Kaipara Harbour.

Trochaclis morningtonensis Marshall, sp. nov.

(Figures 7, 8)

Description: Shell turbiniform, up to 1.80 mm wide, slightly broader than high, spire about 0.64 \times as high as aperture, of moderate thickness, glossy, narrowly umbilicate.

Protoconch 270 μ m wide; sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.60 convex whorls, a weak varix immediately after protoconch, smooth apart from crowded collabral growth lines, base evenly rounded into umbilicus. Umbilicus deep, narrow, not invaded by inner lip, a weak thread descending steeply from within. Aperture subcircular. Inner and outer lips thin. Parietal area of moderate width, glaze very thin.

Type data: Holotype MV.143573 (1.75 \times 1.80 mm, 2.60 teleoconch whorls) and paratype AMS C.160405 (1.70 \times 1.80 mm, 2.50 teleoconch whorls): Fossil Beach, Balcombe Bay, near Mornington, Port Phillip, Victoria, R. Lukey and J. Kerslake; Balcombian (Late Miocene).

Distribution: Late Miocene (Balcombian) of Victoria, Australia.

Remarks: *Trochaclis morningtonensis* is distinctive among *Trochaclis* species in the combination of small protoconch

(width 270 μm), lack of an angulation on the first teleoconch whorl, lack of basal spiral cords, and narrow deep umbilicus with broadly rounded rim.

Etymology: From the township near the type locality.

Trochaclis calva Marshall, sp. nov.

(Figures 9, 10; Table 3)

Description: Shell up to 2.20 mm high, about as high as broad, spire about $0.60\times$ as high as aperture, of moderate thickness, narrowly umbilicate, glossy, translucent white.

Protoconch 300–330 μm wide, tip of apical fold pinched, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.75 convex whorls, a broad, rounded varix immediately after protoconch, smooth apart from crowded collabral growth lines. Umbilicus narrowly crescentic, rim tightly rounded and with fine angulate thread that descends steeply from within. Aperture subcircular; outer lip thin at rim, thicker within; parietal lip thin; inner lip thick.

Animal unknown.

Type data: Holotype (M.117512) and 2 paratypes NMNZ: AUZ53 34°00'S, 171°55'E, Three Kings Trough, north of Three Kings Islands, dead, 805 m, 17 September 1962, R.N.Z.F.A. *Tui*.

Distribution: Off Three Kings Islands, northern New Zealand, 805 m, on comminuted bryozoan/shell substratum.

Remarks: *Trochaclis calva* resembles the Mediterranean species *T. versiliensis* Warén, Carrozza & Rocchini, 1992 in shape, differing primarily in lacking a spiral thread on the first teleoconch whorl, and in having only a single spiral thread beside the umbilicus.

Etymology: Smooth (Latin).

Trochaclis regalis Marshall, sp. nov.

(Figures 11, 12, 15; Table 4)

Description: Shell turbiniform, up to 1.68 mm wide, about as wide as high, spire about $0.60\times$ as high as aperture, of moderate thickness, narrowly umbilicate, glossy, translucent white.

Protoconch 230–280 μm wide, tip of apical fold pinched, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of up to 2.6 convex whorls, a broad rounded varix immediately after protoconch. First 1.5–1.75 whorls with rounded spiral cord that surmounts shoulder angulation, subsequent whorls smooth, fine, crowded collabral growth lines throughout. Umbilicus narrow, deep, fully

Table 3

Trochaclis calva Marshall, sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
<i>1.95</i>	<i>1.90</i>	<i>1.02</i>	<i>2.50</i>	<i>AUZ 53</i>
2.20	2.10	1.04	2.75	AUZ 53
2.20	2.15	1.02	2.70	AUZ 53

open, rim tightly rounded, encircled by two crisp, rounded spiral cords with broad, shallowed concave interspace, innermost cord descending steeply from within. Aperture subcircular; outer lip thin at rim, thicker within; parietal glaze thin; inner lip of moderate thickness.

Animal unknown.

Type data: Holotype M.117510 and paratype NMNZ: BS 640 (P543), 34°05.9'S, 171°55.1'E, off Three Kings Islands, dead, 710 m, 27 June 1978, R/V *Tangaroa*. Paratypes (2 NMNZ): BS 642 (P574), 34°06.5'S, 172°04.7'E, dead, 310 m, 30 June 1978, R/V *Tangaroa*; BS 634 (P462), 34°17.6'S, 171°45.3'E, dead, 427 m, 21 June 1978, R/V *Tangaroa*.

Distribution: Off Three Kings Islands, northern New Zealand, 310–710 m, dead on comminuted bryozoan/shell substratum.

Remarks: *Trochaclis regalis* is exceedingly similar to *T. versiliensis* Warén, Carrozza & Rocchini, 1992 (in Warén, 1992:180, figs. 26E, 36A–D) from the Mediterranean and adjacent Atlantic. The only difference that I am able to detect is in the degree of persistence of the spiral thread on the early teleoconch whorls, which extends over 1.5–1.75 whorls in *T. regalis* as against about 1.25 whorls in *T. versiliensis*. Since no Atlantic archaeogastropods are known to be conspecific with New Zealand ones, it is anticipated that additional differences will be found when the animals can be compared.

Etymology: Royal (Latin), alluding to the type locality.

Trochaclis elata Marshall, sp. nov.

(Figures 13, 14; Table 5)

Description: Shell turbiniform, up to 1.62 mm high, higher than broad, spire $0.52\text{--}0.71\times$ as high as aperture, of moderate thickness, anomphalous, glossy, translucent white.

Protoconch 270–300 μm wide, tip of apical fold pinched, apertural rim slightly flared, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces.

Teleoconch of up to 2.70 convex whorls, a broad, rounded varix immediately after protoconch, first whorl strongly convex, subsequent whorls more weakly convex, periphery evenly rounded, base weakly convex. Smooth apart from fine, crowded collabral growth lines. Aperture subcircular;

Table 4

Trochaclis regalis Marshall, sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.22	1.27	0.96	2.10	BS 634
1.50	1.68	0.89	2.50	BS 640
<i>1.58</i>	<i>1.63</i>	<i>0.97</i>	<i>2.60</i>	<i>BS 640</i>

outer lip thin at rim, thicker within; parietal glaze of moderate thickness; inner lip thick.

Animal unknown.

Type data: Holotype NMNZ M.92197: BS 633 (P461), 34°20.4'S, 171°48.2'E, off Three Kings Islands, dead, 440 m, 21 June 1978, R/V *Tangaroa*. Paratypes (3 NMNZ): AUZ53, 34°00'S, 171°55'E, dead, 805 m, 17 September, 1962, R.N.Z.F.A. *Tui* (2); BS 642 (P574), 34°06.5'S, 172°04.7'E, dead, 310 m, 30 June 1978, R/V *Tangaroa*.

Distribution: Off Three Kings Islands, northern New Zealand, 310–805 m (dead) on comminuted bryozoan/shell substratum.

Remarks: *Trochaclis elata* is extremely similar to the Lower Miocene species *T. bucina* (Laws) from which it differs in being more broadly conical and in having a more open sculptural network on the protoconch.

Etymology: High (Latin).

Trochaclis attenuata Marshall, sp. nov.

(Figures 18, 19)

Description: Shell (holotype) turbiniform, 1.70 mm high, higher than wide, spire slightly higher than aperture, of moderate thickness, anophalous, glossy, translucent white.

Protoconch 270 μ m wide, tip of apical fold pinched, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces; rim sharply defined, not thickened.

Teleoconch of 3.3 convex whorls, a broad, rounded varix immediately after protoconch, first whorl strongly convex, subsequent whorls more weakly convex, periphery rounded, base weakly convex. Smooth apart from fine, crowded collabral growth lines. Aperture subcircular; outer lip thin at rim, thicker within; parietal glaze of moderate thickness; inner lip thick.

Animal unknown.

Type data: Holotype NMNZ M.117516 (1.70 \times 1.25 mm, 3.30 teleoconch whorls): BS 633 (P461), 34°20.4'S, 171°48.2'E, off Three Kings Islands, dead, 440 m, 21 June 1978, R/V *Tangaroa*.

Distribution: Off Three Kings Islands, northern New

Zealand, 440 m (dead), on comminuted bryozoan/shell substratum.

Remarks: Compared with *Trochaclis elata*, which it much resembles, *T. attenuata* differs in being more narrowly conical, in being smaller relative to the number of whorls (height 1.70 mm : 3.3 teleoconch whorls instead of 1.62 mm : 2.70 teleoconch whorls), and in having a considerably more open sculptural network on the protoconch.

Etymology: Drawn out (Latin).

Trochaclis cristata Marshall, sp. nov.

(Figures 16, 17)

Description: Shell turbiniform, up to 1.55 mm wide, slightly wider than high, spire 0.90 \times as high as aperture, of moderate thickness, narrowly umbilicate, glossy, translucent white.

Protoconch 250–270 μ m wide, tip of apical fold pinched, apertural rim simple, sculptured with network of fine, crisp threads that enclose irregular polygonal spaces.

Teleoconch of up to 2.80 whorls, a strong rounded varix immediately after protoconch, with sharp projecting shoulder and peripheral angulations; sutural ramp broad, more or less flat, horizontal on first whorl, shoulder angulation gently descending to about adapical third; side shallowly concave, almost vertical; outer base flat, tightly rounded at inner third. Spire whorls with extremely fine granules, most densely crowded on ramp; fine, crowded collabral growth lines throughout. Umbilicus deep, very narrow, fully open, rim a sharp angulation that descends steeply from within. Aperture subcircular; outer lip thin at rim, thicker within; parietal glaze very thin; inner lip thin, strongly thickened abapically.

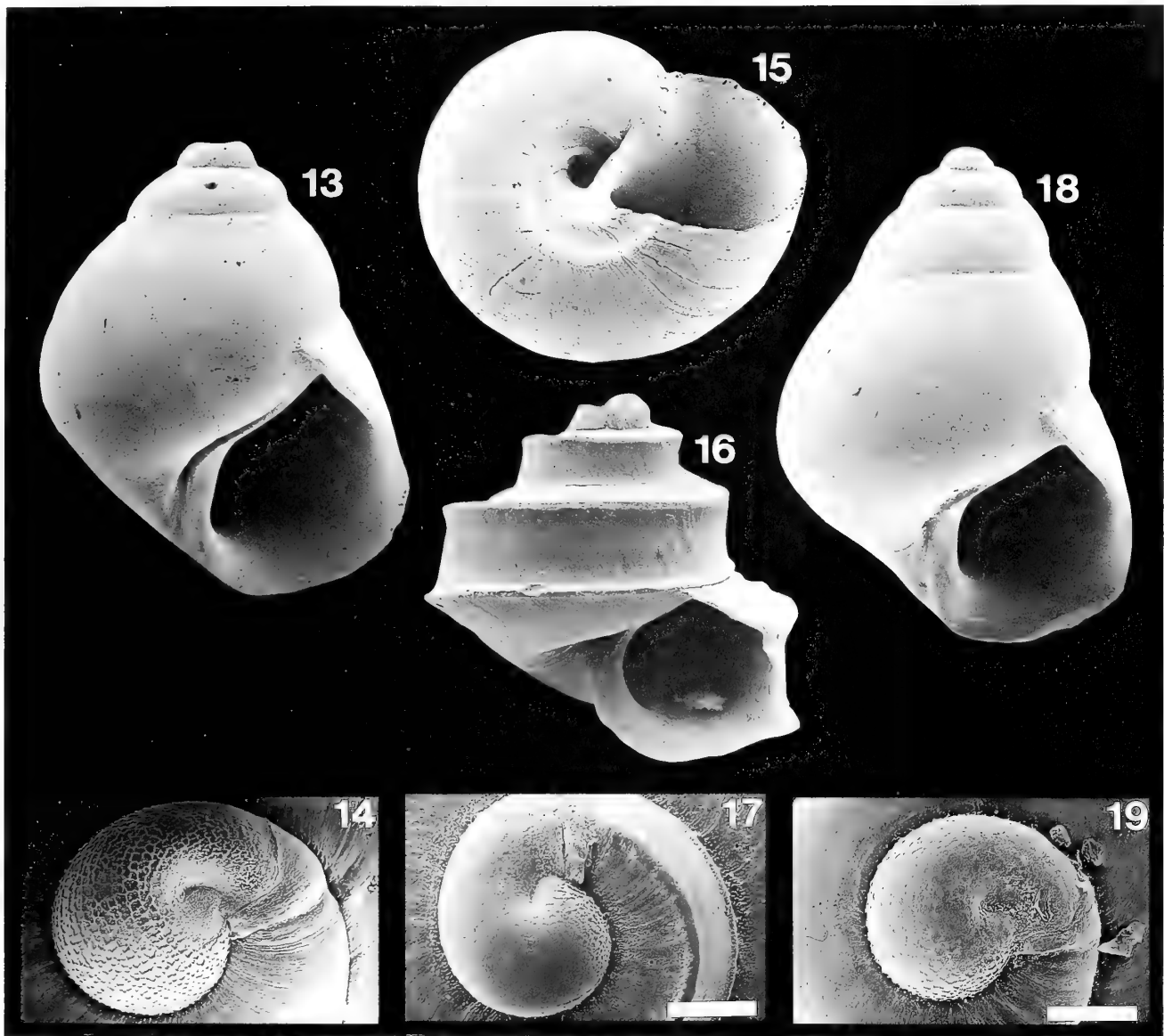
Animal unknown.

Type data: Holotype M.117518 (1.47 mm \times 1.55 mm, 2.80 teleoconch whorls) and juvenile paratype (1.18 mm \times 1.23 mm, 2.25 teleoconch whorls) NMNZ: BS 640 (P543), 34°05.9'S, 171°55.1'E, 24 km NW of Three Kings Islands, dead, 710 m, 27 June 1978, R/V *Tangaroa*.

Distribution: Off Three Kings Islands, northern New Zealand, 710 m, dead on comminuted bryozoan/shell substratum.

Remarks: *Trochaclis cristata* has a much stronger shoulder angulation than any known *Trochaclis* species, and is unique in having a peripheral keel. Shell features are otherwise typical of the genus. If this species is indeed referable to *Trochaclis*, the teleoconch sculpture may indicate derivation of the genus from strongly sculptured stock resembling *Acremodontina* and *Acremodonta* species, perhaps their stem group. Confirmation of its relationships, however, must await discovery of living specimens and study of the radula.

Etymology: Ridged (Latin).



Explanation of Figures 13 to 19

Figures 13–19. *Trochaclis* species. Scales 100 μ m.

Figures 13, 14. *Trochaclis elata* Marshall, sp. nov. Fig. 13. Holotype, off Three Kings Islands, northern New Zealand, 440 m, shell height 1.62 mm. Figure 14. Paratype (NMNZ M.117514), off Three Kings Islands, 310 m.

Figure 15. *Trochaclis regalis* Marshall, sp. nov., holotype, off Three Kings Islands, northern New Zealand, 710 m, shell width 1.63 mm.

Figures 16, 17. *Trochaclis cristata* Marshall, sp. nov., holotype, off Three Kings Islands, northern New Zealand, 710 m, shell height 1.47 mm.

Figures 18, 19. *Trochaclis attenuata* Marshall, sp. nov., holotype, off Three Kings Islands, northern New Zealand, 440 m, shell height 1.70 mm.

Acremodontina Marshall, gen. nov.

Type species: *Conjectura carinata* Powell, 1940; Recent, northern New Zealand.

Etymology: Diminutive of genus group name *Acremodonta* Marshall.

Diagnosis: Shell turbiniform, up to 2.67 mm high, glossy, umbilicus invaded by inner lip, extremely thin internal aragonitic layer present, not visibly nacreous. Protoconch with minute granules, punctations and/or few spiral threads. Teleoconch smooth or with spiral cords, threads, or dashlike spiral grooves. Radula formula $\infty + (2?)4 -$

Table 5

Trochaclis elata Marshall, sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (n)	Station no.
1.52	1.27	1.19	2.50	AUZ 53
1.57	1.37	1.15	2.50	AUZ 53
<i>1.62</i>	<i>1.37</i>	<i>1.18</i>	<i>2.70</i>	<i>BS 663</i>

5 + 1 + 5 - 4(2?) + ∞; central and lateral teeth scalelike, cusplless, longer than broad; tips of marginal teeth deeply split to form two primary branches, one in front of the other, each primary branch with terminal fan of fine, repeatedly branched cusps.

Remarks: The radula in *Acremodontina* species differs from those in *Trochaclis* and *Acremodonta* in having short, scalelike central and lateral teeth. The radula differs further from that in *Trochaclis* (Warén, 1992:fig. 37A) in that each of the marginal teeth has a double terminal cusp fan, and from that in *Acremodonta* in that the teeth are considerably less slender with less finely divided cusps. The protoconch in *Acremodontina* species lacks the crowded wavy threads of *Acremodonta* and the fine reticulate sculpture of *Trochaclis* species. Although several *Acremodontina* species have an axial varix on the first quarter teleoconch whorl, the varix is much further from the protoconch than in any *Trochaclis* species. This group is somewhat intermediate between *Trochaclis* and *Acremodonta* in shell morphology.

A. carinata (Powell, 1940), *A. atypica* (Powell, 1937), and *A. poutama* (E. C. Smith, 1962) were originally referred to *Conjectura* Finlay, 1926, the type species of which (*Crossea glabella* Murdoch, 1905), however, has a vitreous shell and a smooth protoconch of 1.5 whorls (personal observation). Although the animal of *C. glabella* is unknown, it is almost certainly a vitrinellid.

A. simplex (Powell, 1937) and *A. translucida* (May, 1915) were originally referred to *Cirsonella* Angas, 1877 (type

Table 6

Acremodontina maxwelli Marshall, gen. & sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (n)	Station no.
0.83	0.87		1.60	GS 9730
0.87	0.90		1.70	GS 9730
0.87	0.93		1.60	GS 9730
<i>1.23</i>	<i>1.30</i>		<i>2.10</i>	<i>GS 9730</i>

species *Cirsonella australis* Angas, 1877), but the shell, radula, and operculum are entirely different in that genus (Warén, 1992).

Acremodontina maxwelli Marshall, sp. nov.

(Figures 23, 24; Table 6)

Description: Shell turbiniform up to 1.30 mm wide, about as wide as high, rather thin, spire up to 0.54 × as high as aperture, glossy, umbilicus a narrow chink.

Protoconch 230 μm wide, distinctly tilted, rim slightly flared, minutely granulate, with three fine spiral threads.

Teleoconch of up to 2.10 whorls. Shoulder angulation sharp, becoming obsolete on last adult whorl; ramp flat, horizontal at first, becoming gently sloping, side and base rather evenly convex. End of first eighth whorl traversed by a strong, rounded axial varix that is closely followed by sharply defined growth scar. Sculpture of strong, rounded, widely spaced spiral cords that multiply by intercalation, interspaces concave. Shoulder angulation, supra-sutural, and intermediate spirals similar, commencing immediately, continuity disrupted at varix and growth scar on first whorl. Secondary spirals enlarging to resemble primaries, three on ramp, one in each primary spiral interspace on side. Median ramp spiral commencing late on first half whorl, other ramp spirals and side spirals commencing on second whorl. Basal spirals numbering nine in holotype (adult?), innermost two weaker, innermost bordering umbilicus. Umbilicus narrow, partly invaded by

Explanation of Figures 20 to 31

Figures 20–31. *Acremodontina* species. Scales 100 μm.

Figures 20–22, 29, 30. *Acremodontina carinata* (Powell, 1940). Figures 20, 22, 29, 30. Off Three Kings Islands, northern New Zealand, 221–206 m, NMNZ M.92195, shell heights 1.60 mm and 1.53 mm respectively. Figure 21. Off Three Kings Islands, 310 m, NMNZ M.92420, shell height 1.12 mm.

Figures 23, 24. *Acremodontina maxwelli* Marshall, gen. & sp. nov., holotype, Early Miocene, Pakaurangi Point, Kaipara Harbour, New Zealand, shell height 1.23 mm.

Figures 25–28, 31. *Acremodontina varicosa* Marshall, gen. & sp. nov. Figures 28, 31. Holotype, off Three Kings Islands, northern New Zealand, 710 m, shell height 1.50 mm. Figure 25. Paratype (NMNZ M.92198), off Three Kings Islands, 710 m, shell height 1.90 mm. Figure 26. Early Pliocene, Motutapu Point, Pitt Island, Chatham Islands, New Zealand, NZGS TM7669, shell height 1.00 mm. Figure 27. Paratype (NMNZ M.92448), off Three Kings Islands, 805 m, shell height 2.67 mm.

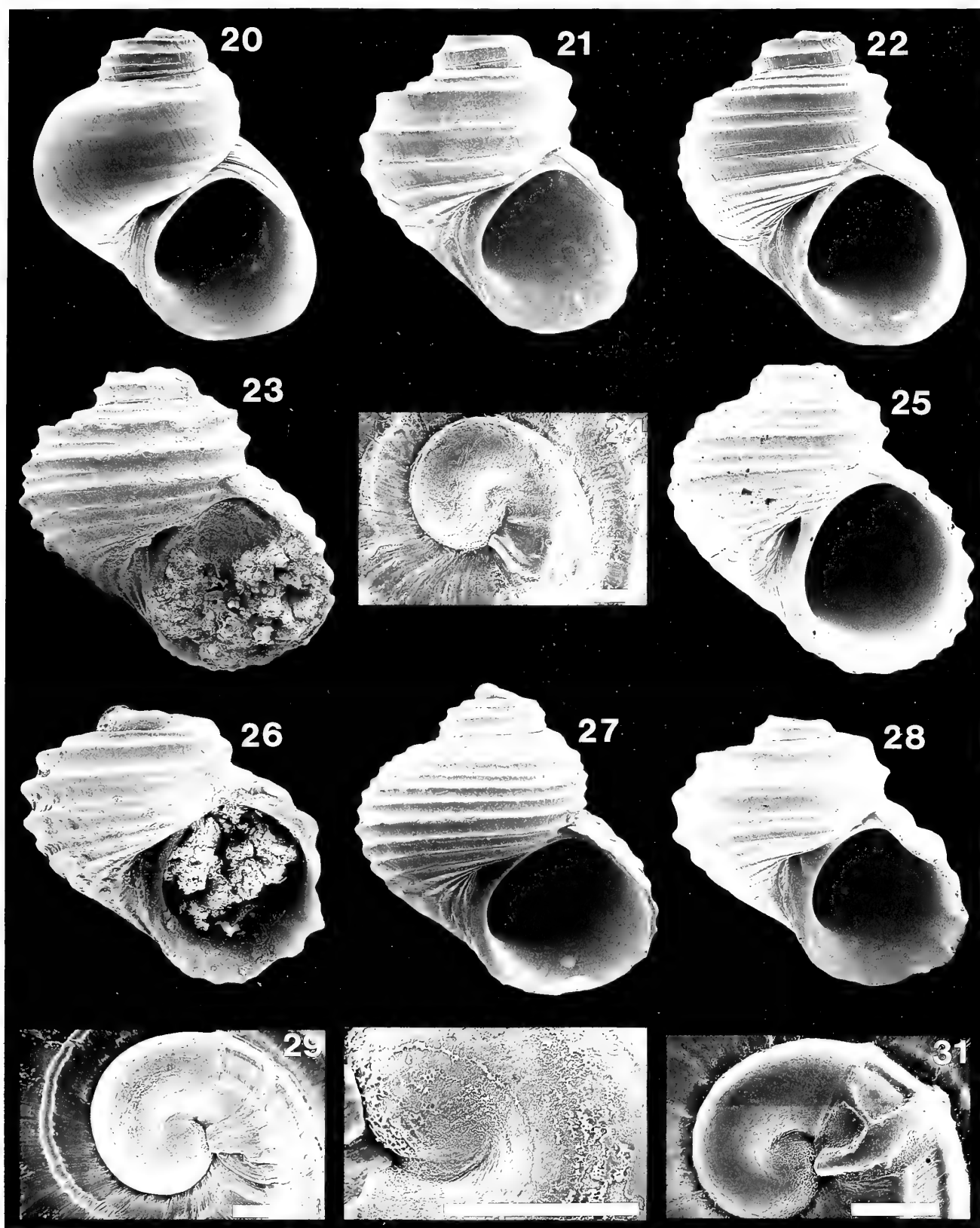


Table 7

Acremodontina carinata (Powell, 1940).
Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.47	1.45	1.01	2.10	BS 897
1.53	1.60	0.96	2.20	BS 897
1.58	1.47	1.07	2.25	BS 897
1.60	1.53	1.04	2.30	BS 897
1.62	1.50	1.08	2.25	BS 897
1.73	1.65	1.05	2.30	BS 894
1.73	1.71	1.01	2.30	BS 897
1.85	1.70	1.09	2.50	BS 897
2.17	1.98	1.09	2.50	BS 894

inner lip. Aperture subcircular; outer lip thin at rim, thicker within; inner lip of moderate thickness.

Type data: Holotype NZGS TM7668 and 3 paratypes (1 NMNZ, 2 NZGS): GS 9730, tuffaceous siltstone, small bay ca. 1.6 km NW of Pakaurangi Point, Kaipara Harbour, northern New Zealand, map ref. Q8/262513 (f9828), March 1979, B. A. Marshall and P. A. Maxwell; Otaian (Early Miocene).

Distribution: Early Miocene (Otaian), Pakaurangi Point, Kaipara Harbour, northern New Zealand.

Remarks: *Acremodontina maxwelli* closely resembles *A. varicosa* n. sp. in general facies, including the presence of a strong varix on the first quarter whorl, but differs from this Recent species in having three spiral cords on the ramp instead of one or occasionally two, and in being substantially smaller relative to the number of whorls.

Etymology: After Philip Maxwell of Waimate (formerly NZGS).

Acremodontina carinata (Powell, 1940)

(Figures 20–22, 29, 30, 56–59; Table 7)

Conjectura carinata Powell, 1940:223, pl. 28, fig. 8; Powell 1979:74, pl. 20, fig. 22.

Description: Shell turbiniform, up to 2.17 mm high, usually slightly higher than broad, rather thin but not fragile, spire 0.62–0.68 × as high as aperture, glossy, translucent, umbilicus a crescentic chink. Protoconch pale buff or colorless, most of first teleoconch whorl colorless, subsequent whorls pale pink, occasionally white.

Protoconch 250–270 μm wide, slightly tilted, rim slightly flared. Sculpture of minute irregular granules that coalesce to form few spiral lirae and broader median spiral band, coalescent granules at outer side of tip of apical fold enclosing minute circular spaces, elsewhere more finely granulate.

Teleoconch of up to 2.50 whorls, last part of last whorl

descending at maturity; shoulder angulation sharp, usually becoming obsolete early on last adult whorl, occasionally persisting; ramp flat, almost horizontal on first whorl, becoming gently sloping; side and base rather evenly rounded. Two close, more or less distinct, simple growth scars on first quarter whorl. Sculpture of narrow, prominent, rounded, crisply defined spiral cords that multiply by intercalation, usually becoming obsolete early on last adult whorl, occasionally persisting to adult apertural rim. Shoulder angulation, suprasutural and intermediate spirals commencing immediately, similar, remaining at similar size throughout. Secondary spirals commencing at varying stages of growth, becoming almost as large as primaries, one or two on ramp, one between median and suprasutural spiral, occasionally one between shoulder and median spiral. Basal spirals similar to spire spirals, numbering up to seven in adults with persistent spirals, though absent in most adults. Umbilicus invaded by inner lip callus at early stage of growth, a narrow crescentic chink; rim tightly rounded, surmounted by spiral thread, often another thread immediately within. Aperture subcircular; outer lip thin at rim, thicker within; inner lip of moderate thickness.

Animal (partially reconstituted from dry). Head dorsoventrally flattened; snout subrectangular, longer than broad; cephalic tentacles stout, large black eyes at outer bases. Operculum pale buff, thin.

Radula (Figures 56–59) with the formula $\infty + 4 + 1 + 4 + \infty$. Central and lateral teeth thin in section, subtrapezoidal, tips bevelled and irregular. Marginals numerous, very slender; innermost pair shorter than others and with smaller cutting area. Tips of inner marginal teeth deeply split to form two primary branches, one in front of the other, each primary branch with curved terminal fan of slender, repeatedly dividing cusps, shorter frontal fan overhanging a prominent projection. Outermost four teeth fused at bases, repeatedly and very deeply divided to form long, slender cusps.

Type data: Holotype (1.13 × 1.10 mm, 2.00 teleoconch whorls) Auckland Institute and Museum 72052: between Spirits Bay and Three Kings Islands, northern New Zealand, 91 m, J. A. Bollons.

Other material examined: Off Three Kings Islands northern New Zealand (93 specimens in 19 lots NMNZ); BS 869, 34°42.6'S, 173°14.4'E, off Rangaunu Bay, dead, 63 m, 27 January 1981, R/V *Tangaroa* 1 (NMNZ); NE of Uruapukapuka Island, Bay of Islands, dead, 27–37 m, February 1970, J. & M. Hancock (1 NMNZ); BS 770, 37°33.4'S, 178°48.3'E, Ranfurly Bank, East Cape, dead, 106–103 m, 25 January 1979, R/V *Tangaroa* (1 NMNZ).

Distribution: Vicinity of Three Kings Islands, and north-eastern North Island, New Zealand, 27–805 m, living at 88–221 m on bryozoan/shell substratum with abundant sponges, hydroids, corals, and gorgonians.

Remarks: Compared with the Australian species *Acremodontina alazon* (Hedley, 1905), which it much resembles, *A. carinata* differs in having a broader protoconch (width 250–270 μm instead of 200 μm) and in being smaller relative to the number of whorls.

Acremodontina varicosa Marshall, sp. nov.

(Figures 25–28, 31; Table 8)

Description: Shell turbiniform, up to 2.67 mm high, usually slightly wider than high, summit flattened, protoconch and often start of first teleoconch whorl distinctly tilted, spire 0.52–0.70 \times as high as aperture, thin but not fragile, glossy, translucent white, umbilicus a narrow chink.

Protoconch 230–250 μm wide, rim slightly flared, with two fine spiral lirae, minutely pitted, tip of apical fold minutely roughened.

Teleoconch of up to 2.70 whorls. Shoulder angulation sharp, becoming obsolete on last adult whorl; ramp flat, horizontal at first, becoming gently sloping; side and base rather evenly convex. End of first quarter whorl traversed by strong, rounded axial varix that is closely followed by sharply defined growth scar. Sculpture of strong rounded, widely spaced spiral cords that multiply by intercalation, interspaces concave. Shoulder angulation, suprasutural and intermediate spirals similar, commencing immediately, slightly offset at growth scar. Secondary spirals enlarging to resemble primaries one on ramp, or occasionally two in each primary spiral interspace, ramp spiral commencing late on first or early on second whorl, other secondaries commencing early or late on last adult whorl. Basal spirals numbering six to eight in adults; innermost weak, bordering umbilicus, others similar. Umbilicus narrow, partly invaded by inner lip. Aperture subcircular; outer lip thin at rim, thicker within; inner lip of moderate thickness.

Animal unknown.

Type data: Holotype (M.117559) and 4 paratypes NMNZ: BS 640 (P543), 34°05.9'S, 171°55.1'E, Three Kings Trough, dead, 710 m, 27 June 1978, R/V *Tangaroa*. Paratypes (23): AUZ 53, 34°00'S, 171°55'E, 805 m, 17 September 1962, R.N.Z.F.A. *Tui* (12 NMNZ, 1 AMS, 1 LACM, 1 MNHN); BS 898 (0644), 34°01.2'S, 171°44.4'E, 206–211 m, 31 January 1981, R/V *Tangaroa* (1 NMNZ); BS 895 (0641), 34°02.0'S, 171°44.0', 246–291 m, 31 January 1981, R/V *Tangaroa* (3 NMNZ); BS 642 (P574), 34°06.5'S, 172°04.7'E, 310 m, 30 June 1978, R/V *Tangaroa* (2 NMNZ); BS 901 (0647), 34°14.1'S, 172°09.0'E, 192–202 m, 1 February 1981, R/V *Tangaroa* (1 NMNZ).

Other material examined: (1 specimen). GS 12163, Whenuataru Tuff, Motutapu Point, Pitt Island, Chatham Islands (CH/f13B), P. A. Maxwell, January 1981; Waipipian (Early Pliocene).

Distribution: Early Pliocene (Waipipian), Pitt Island, Chatham Islands, New Zealand. Recent off Three Kings Islands, northern New Zealand, 192–805 m (dead) on

Table 8

Acremodontina varicosa Marshall, gen. & sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.20	1.30	0.92	1.75	BS 642
1.37	1.67	0.82	2.00	BS 642
<i>1.50</i>	<i>1.77</i>	<i>0.85</i>	<i>2.10</i>	<i>BS 640</i>
1.53	1.73	0.88	2.20	BS 642
1.67	1.80	0.93	2.25	BS 642
1.77	1.87	0.95	2.30	BS 895
1.93	2.05	0.94	2.40	BS 640
2.67	2.57	1.04	2.70	BS 642

comminuted bryozoan and shell substrata with sponges, corals, hydroids and gorgonians.

Remarks: Compared with *Acremodontina carinata*, which it most resembles, *A. varicosa* differs primarily in having a strong varix on the first quarter teleoconch whorl, in having a smaller protoconch (mean width 230 μm instead of 260 μm), and in being consistently white instead of predominantly pale pink. It differs further in that the spiral cords do not become obsolete on the last adult whorl as in most specimens of *A. carinata*, while the shell is usually slightly broader relative to its height. Both species exhibit considerable variation in the number of secondary spiral cords, and in the stage of growth at which particular spirals appear. The two species have overlapping bathymetric ranges and locally occur together as empty shells. Present collections suggest that *A. carinata* ranges into shallower depths (minimum 88 m as against 192 m). The single Early Pliocene specimen from Pitt Island (Figure 26) falls within the range of variation exhibited by Recent specimens and is specifically indistinguishable. *A. carinata* differs from the Australian species *A. alazon* (see below) in having more numerous spiral cords on the spire and base, and a larger protoconch (width 230–250 μm instead of 200 μm).

Etymology: With dilated veins (Latin), alluding to the flared protoconch rim and the varix on the first teleoconch whorl.

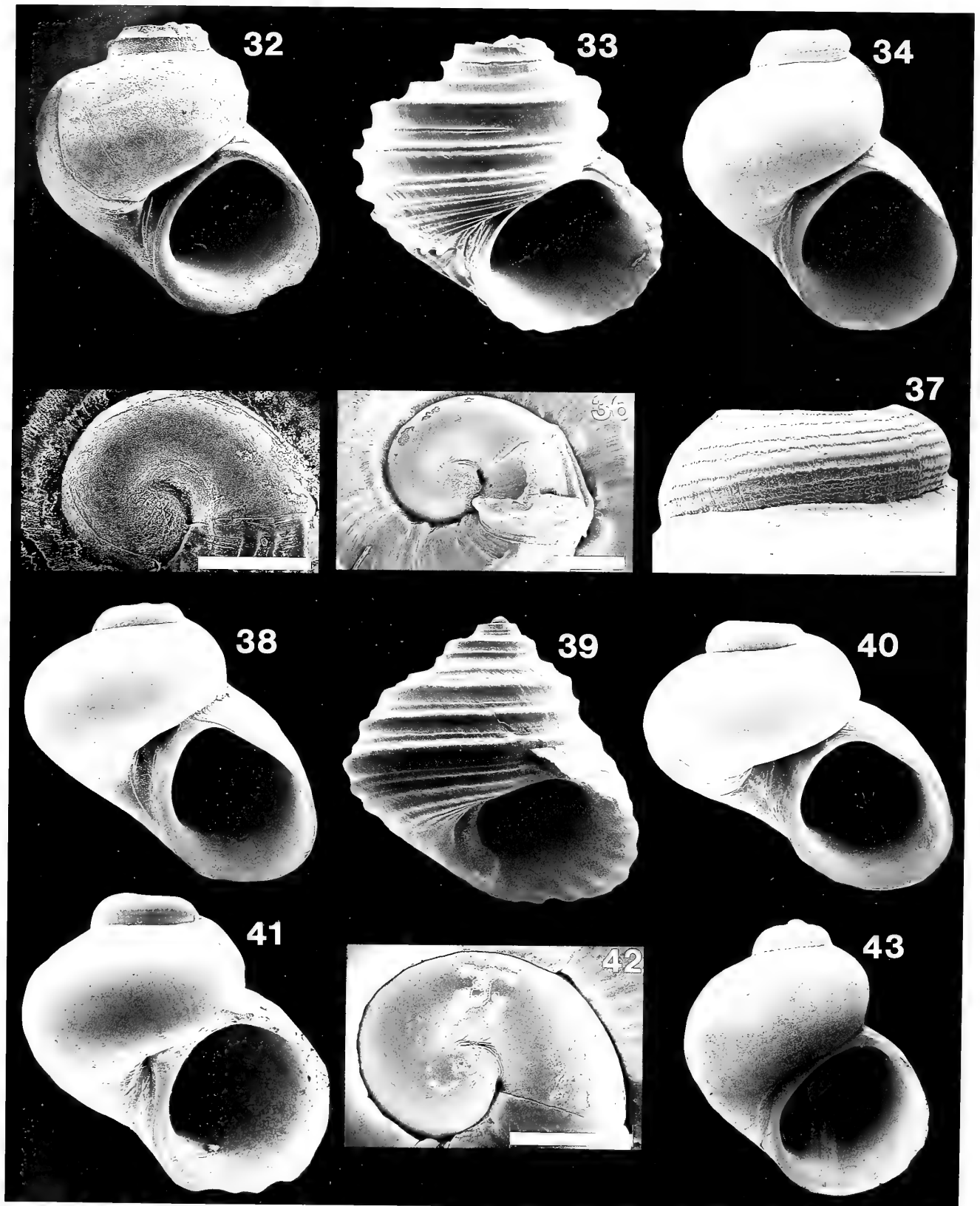
Acremodontina kermadecensis Marshall, sp. nov.

(Figures 32, 60–62)

Description: Shell turbiniform, up to 1.83 mm wide, slightly broader than high, of moderate thickness, spire 0.53–0.70 \times as high as aperture, protoconch and start of first teleoconch whorl gently tilted, glossy, narrowly umbilicate, white.

Protoconch eroded, about 200 μm wide.

Teleoconch of up to 2.4 convex whorls, last part of last whorl descending at maturity. End of first eighth whorl



with prominent axial varix followed by growth scar. Sutural ramp more or less horizontal on first whorl, shoulder angulation descending to about adapical third. Whorls angulated by smooth similar spiral cords, three on side, three on base, becoming obsolete early on last adult whorl. Spire spirals commencing immediately, first surmounting shoulder angulation, second median, third peripheral and bordering suture. Umbilicus narrow, deep, a sharp spiral thread close beside inner edge of tightly rounded rim descends steeply from within. Aperture subcircular; outer lip thin at rim, thicker within; parietal lip thick, becoming almost detached at maturity, continuous with thick inner lip.

Operculum thin, yellowish brown, multispiral.

Radula (Figures 60–62) with the formula $\infty + 5 + 1 + 5 + \infty$. Central and lateral teeth simple, cusplless, laminar, longer than broad, laterals outwardly decreasing in size. Innermost pair of marginal teeth short, without cutting area. Other marginal teeth similar to those of *A. carinata* (see above).

Type data: Holotype M.262496 (1.77 × 1.83 mm, 2.40 teleoconch whorls) and paratype (1.32 × 1.40 mm, 2.10 teleoconch whorls) NMNZ: BS 309, off Bell's Flat, Raoul Island, Kermadec Islands, alive on hard, rugged substratum, 165–220 m, 4 April 1973, R/V *Acheron*.

Distribution: Off Raoul Island, Kermadec Islands, living at 165–220 m, with abundant alcyonarians, gorgonians and sponges.

Remarks: *Acremodontina kermadecensis* resembles *A. alazon* and differs from other species of *Acremodontina* in having only three spiral cords on the spire. It differs from *A. alazon* in having considerably weaker spiral cords, and in having an extra cord on the base. It resembles *A. carinata* in that the spiral cords become obsolete early on the last adult whorl, yet resembles *A. varicosa* and *A. maxwelli* in having a varix early on the first teleoconch whorl. The protoconch, though eroded, appears to be sim-

ilar in width (ca. 200 μ m) to that in *A. alazon*, and smaller than those in other species of *Acremodontina*.

Etymology: From the Kermadec Islands.

Acremodontina boucheti Marshall, sp. nov.

(Figures 33, 36, 63, 64; Table 9)

Description: Shell turbiniform, up to 3.25 mm high, about as broad as high, of moderate thickness, stout, summit flattened, protoconch and early first teleoconch whorl distinctly tilted, spire 0.57–0.61 × as high as aperture, glossy, translucent, colorless, narrowly umbilicate.

Protoconch 230–270 μ m wide, rim weakly flared, surface of tip of apical fold finely roughened, elsewhere smooth.

Teleoconch of up to 2.60 convex whorls. Shoulder angulation sharp, becoming obsolete on last adult whorls, which is rather evenly convex; ramp flat, horizontal on first whorl, thereafter gently sloping; side and base rather evenly convex. End of first eighth whorl traversed by strong, rounded axial varix that is closely followed by sharply defined growth scar. Sculpture of strong, rounded, widely spaced spiral cords that multiply by intercalation, interspaces concave. Shoulder angulation, suprasutural, and intermediate spirals similar, commencing immediately, continuity disrupted by varix and growth scar on first whorl. Secondary spirals rapidly enlarging to resemble primaries, all spirals similar on last adult whorl. Adapical ramp spiral commencing on second half of first whorl; abapical ramp spiral (when present) commencing late second or early third whorl. Secondary spiral between shoulder and median spiral (seldom absent) and that between median and suprasutural spiral commencing on second half of second whorl or early on third whorl. Basal spirals numbering four to, six innermost weaker and bordering umbilicus. Aperture subcircular; outer lip thin at rim, rapidly thickened; inner lip of moderate thickness.

Radula (Figures 63, 64). Central and lateral teeth subrectangular, longer than broad, thin in section, tips cusp-

Explanation of Figures 32 to 43

Figures 32–43. *Acremodontina* species. Scales 100 μ m.

Figure 32. *Acremodontina kermadecensis* Marshall, gen. & sp. nov., holotype, off Raoul Island, Kermadec Islands, 165–220 m, shell height 1.77 mm.

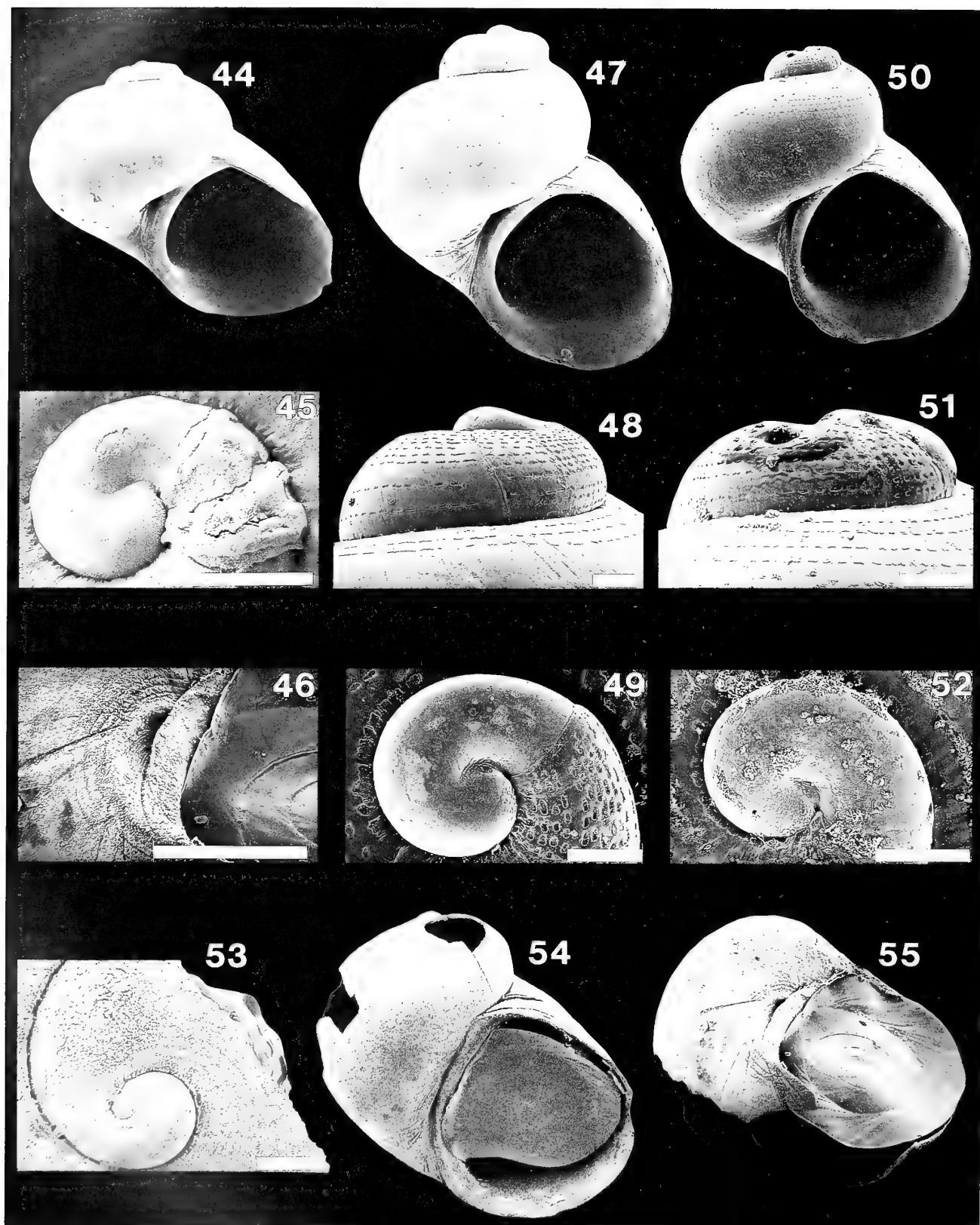
Figures 33, 36. *Acremodontina boucheti* Marshall, gen. & sp. nov., holotype, off southern New Caledonia, 505–515 m, shell height 2.10 mm.

Figures 34, 35, 37. *Acremodontina atypica* (Powell, 1937). Figures 34, 37. Off Three Kings Islands, northern New Zealand, 201–216 m, NMNZ M.92206, shell height 1.50 mm. Figure 35. Off Three Kings Islands, 206–211 m, NMNZ M.92196.

Figures 38, 40–42. *Acremodontina simplex* (Powell, 1937). Figure 38. Off Three Kings Islands, northern New Zealand, 310 m, NMNZ M.92200, shell height 1.65 mm. Figures 40, 42. Off Three Kings Islands, 173–178 m, NMNZ M.92199, shell height 1.10 mm. Figure 41. Off Three Kings Islands, 102 m, NMNZ M.34279, shell height 1.30 mm.

Figure 39. *Acremodontina crassica* (Powell, 1937), off Three Kings Islands, northern New Zealand, 102 m, NMNZ M.34244, shell height 4.05 mm.

Figure 43. *Acremodontina translucida* (May, 1915), paratype, off Thoun Bay, Tasmania, 73 m, AMS C.39470, shell height 2.55 mm.



less. Apparently four pairs of lateral teeth (poorly separated in preparation). Marginal teeth similar to those of *A. carinata* (see above).

Type data: Holotype MNHN, paratype NMNZ: BIOCAL stn DW 66, 24°55'S, 168°22'E, off S New Caledonia, alive, 505–515 m, 3 September 1985, N.O. *Jean-Charcot*. Paratypes (4 MNHN): MUSORSTOM 4 stn DC 168, 18°48'S, 163°11'E, off N New Caledonia, dead, 720 m, 16 September 1985, N.O. *Vauban* (1); BIOCAL stn DW 48, 23°00'S, 167°29'E, off S New Caledonia, dead, 775 m, 31 August 1985, N.O. *Jean-Charcot* (1); CHALCAL 2 stn DW 76, 23°41'S, 167°45'E, off S New Caledonia, dead, 470 m, 30 October 1986, N.O. *Coriolis* (1); SMIB 3 stn DW 01, 24°56'S, 168°22'E, off S New Caledonia, alive, 520 m, 20 May 1987, N.O. *Vauban* (1).

Distribution: Off northern and southern New Caledonia, 470–720 m, living at 505–520 m.

Remarks: Compared with *Acremodontina varicosa*, which it most resembles, *A. boucheti* differs in having a narrower postlarval varix, in attaining larger size, and in that the secondary spiral cords enlarge to resemble the primaries when the shell is larger.

Etymology: After Philippe Bouchet (MNHN).

Acremodontina alazon (Hedley, 1905)

Liotia alazon Hedley, 1905:49, fig. 14.

?*Liotia alazon*. Iredale & McMichael, 1962:678.

Description: Shell (holotype) turbiniform, 1.70 mm wide, slightly broader than high, of moderate thickness, stout, protoconch and early first teleoconch slightly tilted, spire 0.69× as high as aperture, glossy, translucent, colorless, umbilicate.

Protoconch 200 µm wide, rim slightly thickened, sculpture unknown.

Teleoconch of 2.25 convex whorls. End of first eighth whorl with massive axial varix, area between protoconch and varix with three crisp spiral cords. Subsequent spire whorls sculptured with three strong, similar, growth spiral keels. Apical keel forming strong shoulder angulation,

rising above level of protoconch on first whorl; median keel peripheral; summit of apical keel partly covered by succeeding whorls, becoming fully exposed through descent of last half whorl at maturity. Base with three rounded spiral cords, outermost median, innermost weakest and bordering deep, narrow umbilicus. Aperture subcircular. Outer lip thin at rim, thicker within. Inner lip thick, very thick abapically.

Animal unknown.

Type data: Holotype (1.52 × 1.70 mm, 2.25 teleoconch whorls), AMS C.19854, off Cape Byron, northern New South Wales, 203 m.

Distribution: Off Cape Byron, northern New South Wales, Australia, 203 m (dead).

Remarks: *Liotia alazon* is extremely similar to *A. carinata*, *A. varicosa*, *A. boucheti*, *A. kermadecensis*, and *A. maxwelli*, and despite the absence of the diagnostic radula, there can be little doubt that it is a species of *Acremodontina*. The holotype, which remains the only known specimen, was well illustrated by Hedley (1905:fig. 14).

Acremodontina atypica (Powell, 1937)

(Figures 34, 35, 37, 65–67; Table 10)

Conjectura atypica Powell, 1937:187, pl. 41, fig. 10, 11; Powell, 1979:73, pl. 20, fig. 21.

Description: Shell turbiniform, up to 1.70 mm high, usually slightly higher than broad, of moderate thickness, summit flattened, protoconch and early first teleoconch whorl distinctly tilted, spire 0.54–0.80× as high as aperture, glossy, translucent, umbilicus a narrow chink. Apical fold tip and adaxial side of protoconch yellowish brown, elsewhere white.

Protoconch 230 µm wide, rim simple, tip of apical fold finely roughened, elsewhere minutely pitted.

Teleoconch of up to 2.20 whorls, end of last whorl descending at maturity; whorls either rather evenly convex or first 1–1.5 whorls with flat, more or less horizontal ramp, and weak to strong shoulder angulation. First half whorl sculptured with numerous, close, similar, smooth,

←

Explanation of Figures 44 to 55

Figures 44–55. *Acremodontina* and *Austrotrochaclis* species. Scale in Figure 46, 500 µm, others 100 µm.

Figures 44, 55. *Acremodontina magna* Marshall, gen. & sp. nov., holotype, off Three Kings Islands, northern New Zealand, 805 m, shell height 3.35 mm.

Figures 47–49. *Acremodontina poutama* (E. C. Smith, 1962), paratype NMNZ M.19424, off Poutama Island, Stewart Island, 55 m, shell height 1.90 mm.

Figures 50–52. *Acremodontina balcombiana* Marshall, gen. & sp. nov., holotype, Late Miocene, Fossil Beach, Port Phillip, Victoria, shell height 1.50 mm.

Figures 46, 53–55. *Austrotrochaclis ponderi* Marshall, gen. & sp. nov., off Long Reef, Sydney, New South Wales, 38 m. Figures 46, 55. Paratype NMNZ M.262660, shell width 1.70 mm. Figure 53. Paratype AMS 174898. Figure 54. Holotype, shell height 2.00 mm.

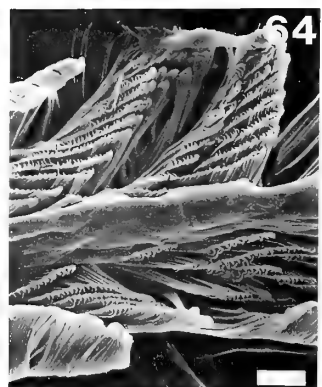
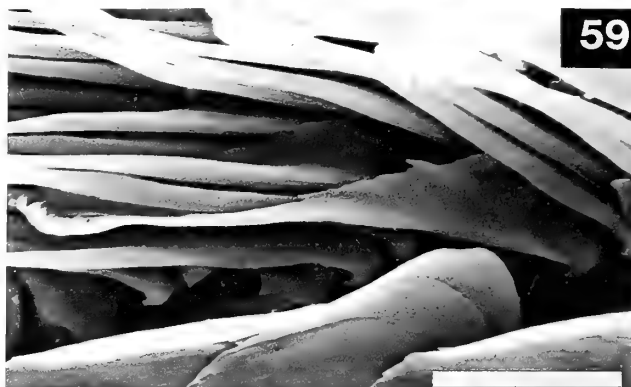
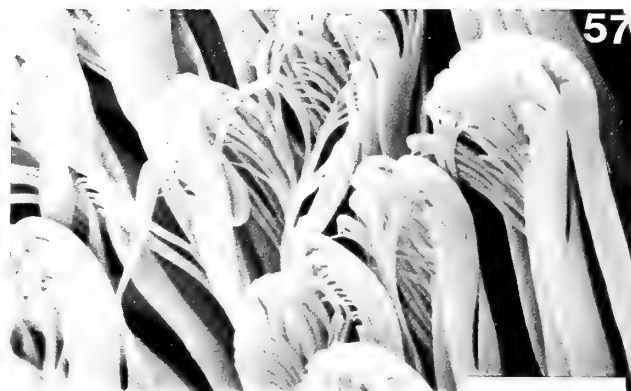


Table 9

Acremodontina boucheti Marshall, gen. & sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleo- conch whorls (<i>n</i>)	Station no.
1.30	1.52	0.85	1.90	SMIB3 DW01
1.90	2.10	0.90	2.25	BIOCAL DW66
<i>2.10</i>	<i>2.20</i>	<i>0.95</i>	<i>2.40</i>	<i>BIOCAL DW66</i>
2.40	2.40	1.00	2.30	CHALCAL 2 DW76
2.82	2.95	0.95	2.50	BIOCAL DW48
3.25	3.15	1.03	2.60	MUSORSTOM 4 DC168

irregularly wavy spiral threads that multiply by intercalation, interspaces with fine, irregular axial riblets and collabral growth lines. Occasional specimens with spiral threads and shoulder angulation persisting onto last adult whorl, and with enlarged spirals, one surmounting shoulder angulation, one or two on side, and two on outer base. Base with two narrow smooth spiral cords beside umbilicus. Umbilicus narrow, partly invaded by inner lip. Aperture subcircular, outer lip thin at rim, thicker within; parietal lip rather thick.

Animal (partially reconstituted from dry). Head dorsoventrally flattened. Snout subrectangular, longer than broad. Cephalic tentacles short, broad, tips rounded, large black eyes at outer bases. Foot medially cleft anteriorly. Operculum thin, chitinous, pale yellowish brown, multi-spiral.

Radula (Figures 65–67) with the formula $\infty + 4 + 1 + 4 + \infty$. Central and lateral teeth narrowly subrectangular, longer than broad, thin in section, tips smooth, cuspless. Marginal teeth similar to those of *A. carinata* (see above).

Type data: Holotype BMNH 1962985 (1.70 × 1.68 mm, 2.20 teleoconch whorls), R.R.S. *Discovery II* sta. 933, 34°13.3'S, 172°12.0'E, off Three Kings Islands, northern New Zealand, 260 m, 17 August 1932.

Table 10

Acremodontina atypica (Powell, 1937). Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)	Station no.
1.25	1.28	0.98	2.00	BS 392
1.25	1.20	1.04	2.00	BS 392
1.35	1.30	1.04	2.00	BS 394
1.42	1.37	1.04	2.10	BS 895
1.42	1.38	1.03	2.10	BS 898
1.43	1.40	1.02	2.00	BS 895
1.50	1.40	1.07	2.20	BS 906
1.57	1.53	1.03	2.20	BS 895
1.63	1.57	1.04	2.10	BS 391
1.70	1.60	1.06	2.20	BS 395

Other material examined: 25 specimens (12 lots NMNZ) from vicinity of Three Kings Islands.

Distribution: Off Three Kings Islands, northern New Zealand, 91–622 m, living at 206–211 m on comminuted bryozoan/shell substratum with sponges, hydroids, corals and gorgonians.

Remarks: *Acremodontina atypica* is strongly characterized by the yellowish brown protoconch, and the numerous fine spiral threads on the early teleoconch. These characters facilitate separation of occasional specimens that approach weakly sculptured forms of *A. carinata* (Figure 20), and that in turn suggest that the species belongs in *Acremodontina*.

Acremodontina magna Marshall, sp. nov.

(Figures 44, 45)

Description: Shell (holotype) 3.80 mm wide, slightly broader than high, of moderate thickness, spire 0.6 × as high as aperture, glossy, translucent white, umbilicus a narrow chink.

Protoconch 300 μm wide, surface slightly etched away, rim thickened.

Teleoconch of 2.75 convex whorls, end of last (adult)

Explanation of Figures 56 to 64

Figures 56–64. Radulae of *Acremodontina* species.

Figures 56–59. *Acremodontina carinata* (Powell, 1940), adult, off Three Kings Islands, northern New Zealand, 221–206 m, NMNZ M.92195. Figure 56. Central and lateral teeth, scale 10 μm. Figure 57. Tips of inner marginal teeth, scale 5 μm. Figure 58. Outermost marginal teeth, scale 10 μm. Figure 59. Innermost marginal tooth, scale 10 μm.

Figures 60–62. *Acremodontina kermadecensis* Marshall, gen. & sp. nov., ex adult holotype. Figure 60. Central, lateral and inner marginal teeth. Figure 61. Inner marginal teeth. Figure 62. Tips of outermost marginal teeth. Scales 5 μm.

Figures 63, 64. *Acremodontina boucheti* Marshall, gen. & sp. nov., ex adult holotype. Figure 63. Tips of outermost marginal teeth. Figure 64. Width of radula. Scales 10 μm.

whorl descending. End of first quarter whorl traversed by a strong, rounded axial varix that is closely followed by sharply defined growth scar. Area between protoconch and varix with three spiral cords. Shoulder spiral strong, vanishing near end of first whorl; median and suprasutural spirals vanishing on first quarter whorl after varix. Subsequent whorls smooth. Umbilical chink bordered by spiral thread that descends steeply from within. Aperture subcircular. Outer lip thin at rim, thicker within. Inner lip and parietal glaze rather thick.

Animal unknown.

Type data: Holotype (3.35 × 3.80 mm, 2.75 teleoconch whorls) NMNZ M.117521: AUZ 53, 34°00'S, 171°55'E, off Three Kings Islands, northern New Zealand, dead, 805 m, 17 September 1962, R.N.Z.F.A. *Tui*.

Remarks: *Acremodontina magna* is rendered highly distinctive by its large size, strong postlarval varix, and absence of sculpture after the first teleoconch whorl. In the absence of the diagnostic radula, this species is referred to *Acremodontina* because the first teleoconch whorl is similar to those of *A. maxwelli*, *A. varicosa*, and *A. boucheti*.

Etymology: Large (Latin).

Acremodontina simplex (Powell, 1937)

(Figures 38, 40–43, 68, 69; Table 11)

Cirsonella simplex Powell, 1937:185, pl. 50, fig. 12; Powell, 1979:71.

Description: Shell turbiniform to depressed-turbiniform, up to 2.17 mm wide, usually slightly wider than high, spire 0.44–1.00× as high as aperture, summit flattened, protoconch and start of first teleoconch whorl often slightly tilted to varying degrees, of moderate thickness, glossy, stout; umbilicus narrow, becoming partly or entirely infilled by inner lip; translucent white.

Protoconch 200–260 μm wide (mean 230 μm), smooth apart from fine wrinkles at tip of rounded apical fold, apertural rim simple.

Teleoconch of up to 2.50 smooth, convex whorls, usually slightly flattened above and below rounded periphery, end of last adult whorl descending, occasionally becoming dissolute. First quarter whorl usually delineated by pronounced growth scar. Umbilical rim tightly rounded, usually defined by fine spiral angulation, usually another fine angulation within; umbilicus narrow, deep, becoming narrowly crescentic and almost or entirely infilled by inner lip callous at varying stages of growth, occasionally remaining open in dissolute adult specimens. Aperture subcircular; outer lip thin at rim, thicker within; parietal and inner lips continuous, thick.

Animal (reconstituted from dry). Foot anteriorly bilobate. Snout dorsoventrally flattened, subrectangular, longer than broad. Cephalic tentacles dorsoventrally flattened, broad, tips rounded; large, deeply pigmented eyes at outer bases. Operculum pale yellowish brown, thin, multispiral.

Radula (Figures 68, 69) with the formula $\infty + 5 + 1 + 5 + \infty$. Central and lateral teeth scalelike, thin in section, subrectangular, cutting edges smooth. Marginal teeth slender, at least 60 per transverse row, similar to those of *A. carinata* (see above).

Type data: Holotype BMNH 1962977 (1.30 mm × 1.52 mm): R.R.S. *Discovery II* st. 933, 34°13.3'S, 172°12.0'E, off Three Kings Islands, dead, 260 m, 17 August 1932.

Other material examined: 79 specimens in 19 lots NMNZ.

Distribution: Off Three Kings Islands and off Great Exhibition Bay, northern New Zealand 78–805 m, living at 78–178 m on comminuted shell and bryozoan substratum with sponges, corals, hydroids and gorgonians.

Remarks: *Acremodontina simplex* is characterized by its smooth, glossy, translucent white shell, and thick inner lip that tends to invade the narrow umbilicus. The species is variable in shape and in the stage at which the umbilicus becomes infilled by the inner lip, and there is complete gradation between extremes. Although Powell's (1937:pl. 50, fig. 12) illustration of the holotype shows what appear to be two spiral cords entering an open umbilicus, the umbilicus in the holotype is in fact filled by the thick inner lip as stated in the original description. Powell's subsequent (1979:71) statement that the umbilicus is almost filled by two crescentic ridges of callus bordering the inner lip is clearly an attempt to reconcile the discrepancy between the original illustration and the description.

Acremodontina translucida (May, 1915)

(Figure 43)

Cirsonella translucida May, 1915:97, pl. 7, fig. 38; May, 1923, pl. 20, fig. 12.

Description: Shell up to 2.65 mm high, slightly higher than broad at maturity, of moderate thickness, spire 0.32–0.60× as high as aperture, glossy, umbilical chink narrow; translucent white with narrow, pale pinkish brown sub-sutural band.

Protoconch 300 μm wide, no obvious microsculpture, apertural rim slightly thickened.

Teleoconch of up to 2.25 evenly convex whorls, last half whorl descending at maturity. Sculpture consisting of spiral rows of narrow, dashlike pits that elongate with increasing shell size, row number progressively reducing in number soon after appearance. Sculpture restricted to first whorl in most specimens, occasionally persisting below periphery onto last adult whorl. Umbilical chink bounded by fine spiral thread. Aperture subcircular, lips simple, parietal and inner lips contiguous, thick.

Animal unknown.

Type data: Holotype (Tasmanian Museum, Hobart, E292/7633) and 5 paratypes (AMS C.39470): off Thouin Bay, eastern Tasmania, dead, 73 m.

Table 11

Acremodontina simplex (Powell, 1937).
Shell measurements (mm) and countings.

Height	Diameter	Height/ diameter	Teleoconch whorls (n)	Station no.
1.02	1.27	0.80	1.90	BS 392
1.10	1.27	0.87	2.00	BS 906
1.33	1.33	1.00	2.10	BS 392
1.33	1.37	0.97	2.25	BS 894
1.40	1.30	1.08	2.30	BS 392
1.52	1.52	1.00	2.10	BS 642
1.65	1.83	0.90	2.30	BS 642
1.70	1.87	0.90	2.25	BS 642
1.80	1.78	1.01	2.30	BS 642
1.83	1.97	0.93	2.40	BS 640
1.85	2.00	0.92	2.30	BS 640
1.93	2.07	0.93	2.25	BS 640
2.00	2.17	0.92	2.50	BS 640

Distribution: Off Tasmania, 73 m.

Remarks: This species is rendered highly distinctive by its rounded teleoconch whorls and sculpture of spiral rows of dashlike pits. It is extremely similar to *Acremodontina poutama* (E. C. Smith, 1962) from off southern New Zealand, and *A. morningtonensis* from the Late Miocene of Victoria (see below). It is referred to Trochacrididae because of the similarity of the shell to that of *A. poutama*, the radula of which is characteristic of the family (Figure 70).

Cotton (1959) recorded the species from King George Sound, Western Australia, and from off South Australia, but not having seen the specimens, I am unable to confirm their identity. I am grateful to Anders Warén, who drew my attention to the probable relationships of this species.

Acremodontina balcombiana Marshall, sp. nov.

(Figures 50–52)

Description: Shell (holotype) 1.50 mm wide, as high as broad, thin, spire 0.75× as high as aperture, glossy, an-omphalous.

Protoconch 250 µm wide, minutely roughened at tip of apical fold, elsewhere minutely pitted, rim simple.

Teleoconch of 2.00 convex whorls, end of last whorl descending at maturity. First whorl sculptured with fine spiral rows of dashlike pits, weakening and vanishing on first half of second whorl, next half whorl smooth. Base with fine, steeply descending spiral angulation close beside inner lip. Aperture subcircular, peristome continuous, lips simple.

Type data: Holotype MV P.143574 (1.50 × 1.50 mm, 2.00 teleoconch whorls): Fossil Beach, Balcombe Bay near Mornington, Port Phillip, Victoria, R. Lukey and J. Kerlake; Balcombian (Late Miocene).

Table 12

Acremodontina poutama (E. C. Smith, 1962).
Shell measurements (mm) and countings (paratypes).

Height	Diameter	Height/ diameter	Teleoconch whorls (n)
1.48	1.58	0.92	2.10
1.73	1.88	0.92	2.00
1.80	1.73	1.04	2.10
1.80	1.77	1.02	2.10
1.83	1.87	0.98	2.00
1.87	1.80	1.04	2.20
1.90	1.78	1.07	2.25
1.90	2.03	0.93	2.00
1.93	2.10	0.92	2.20
2.60	2.23	1.17	2.70
2.63	2.45	1.07	2.40

Distribution: Port Phillip, Late Miocene (Balcombian), Fossil Beach, Victoria, Australia.

Remarks: Compared with *Acremodontina poutama* and *A. translucida* from which it is otherwise indistinguishable, *A. balcombiana* differs in having a smaller protoconch (width 250 µm instead of 270–330 µm mean 300 µm) and a narrower nucleus.

Etymology: From the Balcombian Stage.

Acremodontina poutama (E. C. Smith, 1962)

(Figures 47–49, 70; Table 12)

Conjectura poutama E. C. Smith, 1962:50, fig. 1, 1a; Powell, 1979:74.

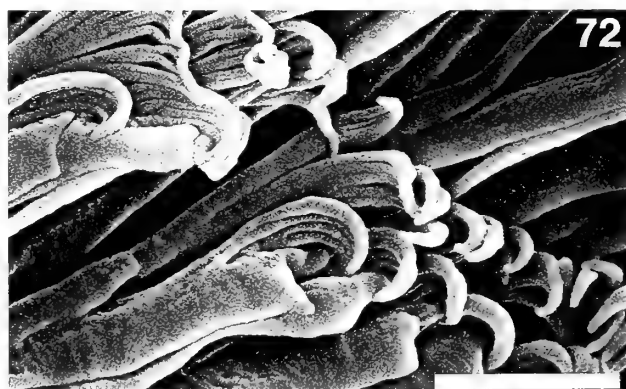
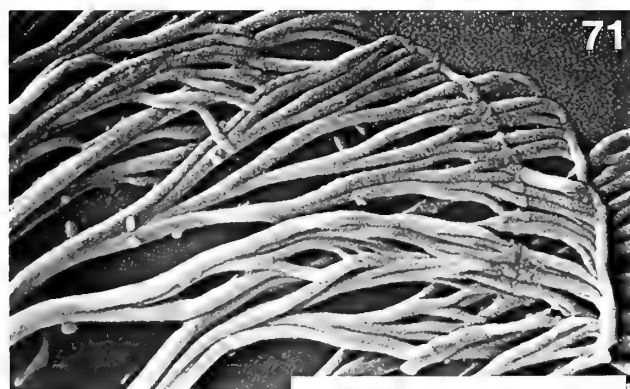
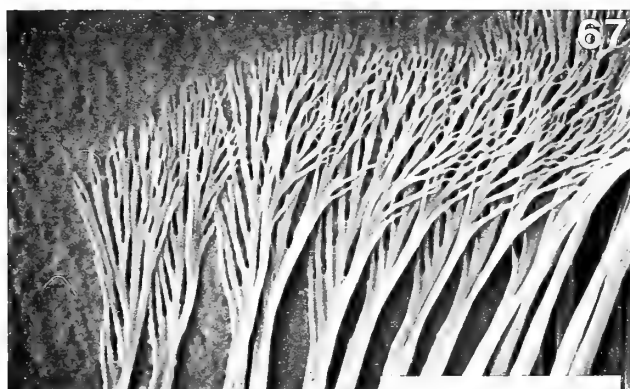
Description: Shell up to 2.63 mm high, about as high as broad, thin but not fragile, spire 0.57–0.88× as high as aperture, narrow umbilicus invaded by inner lip, glossy, translucent, colorless.

Protoconch 270–330 µm wide (mean 300 µm), usually slightly tilted, minutely roughened at outer part of tip of apical fold, elsewhere minutely punctate, rim simple.

Teleoconch of up to 2.70 rather evenly convex whorls, end of last whorl descending at maturity. First half whorl, first whorl, or sometimes all whorls with spiral rows of narrow dashlike pits, rows beginning to reduce in number soon after their appearance, pits gradually elongating. Umbilicus narrow, a fine spiral thread at rim, reduced to an elliptical chink through partial or complete invasion by inner lip. Aperture subcircular; outer lip thin at rim, thicker within; inner lip of moderate thickness.

Radula (Figure 70). Central and lateral teeth narrowly rectangular, scalelike, at least two pairs of lateral teeth (poorly separated in preparation). Marginal teeth similar to those in *A. carinata* (see above).

Type data: Holotype (M.20251) and many paratypes NMNZ: off Poutama Island, South Cape, Stewart Island,



New Zealand, 55 m, June 1955, bryozoan shell-sand (1 paratype taken alive).

Other material examined: (8 specimens NMNZ). BS 974, Charles Sound, 26 m, 10 February 1987, G. S. Hardy (1); off Port Adventure, Stewart Island, dead, 55 m, October 1952 (5); off Puysegur Point, SW Otago, dead, 183 m, J. Bollons (1); BS 938, off Snares Islands, dead, 33–37 m, 6 December 1984, G. S. Hardy & A. L. Stewart (1).

Distribution: Southern Westland, Stewart Island, and Snares Islands, southern New Zealand, on comminuted bryozoan/shell substratum, 55–183 m, living at 55 m.

Remarks: This species is referred to Trochaclididae because the radula is similar to that of *Acremodontina* species. *A. poutama* is exceedingly similar to *A. translucida*, and the only difference I am able to detect is the presence of a subsutural color band in the Tasmanian species. They may in fact be conspecific, though I prefer to maintain the separation until animals and radulae can be proven to be identical.

Genus *Acremodonta* Marshall, 1983

Acremodonta Marshall 1983:127. Type species (by original designation): *Thoristella crassicosta* Powell, 1937; Recent, northern New Zealand.

Diagnosis: Shell very large for the family (up to 6.10 mm wide), trochiform, anomphalous, stout, glossy, internally strongly nacreous. Protoconch sculptured with wavy spiral threads, teleoconch with rounded spiral cords that multiply by intercalation. Central and lateral teeth (if actually present) similar to marginals. Marginal teeth very slender, tips repeatedly branching. Edge of oral shield with elongate, dendritic papillae. Ctenidium bipectinate, with free tip and relatively long afferent membrane.

Acremodonta crassicosta (Powell, 1937)

(Figure 39)

Thoristella crassicosta Powell, 1937:178, pl. 49, figs. 14, 15; Powell, 1979:59, pl. 17, fig. 5.

Table 13

Austrotrochaclis ponderi Marshall, gen. & sp. nov. Shell measurements (mm) and countings. Holotype in italics.

Height	Diameter	Height/ diameter	Teleoconch whorls (<i>n</i>)
1.43	1.68	0.85	1.50
1.57	1.73	0.90	1.50
2.05	2.07	0.99	1.80

Acremodonta crassicosta. Marshall, 1983:127, figs. 1A, B, 2A–E; Hickman & McLean, 1990, figs. 93a–f.

Type data: Holotype BMNH 1962958, 34°13.3'S, 172°12.0'E, off Three Kings Islands, 260 m, 17 August 1932, R.R.S. *Discovery II*.

Other material examined: 105 specimens in 22 lots NMNZ.

Distribution: Off Three Kings Islands, northern New Zealand, 102–805 m, living at 173–256 m on comminuted bryozoan-shell substrata with sponges, hydroids, gorgonians and corals.

Remarks: The shell and radula were described and illustrated by Marshall (1983), and the external anatomy by Hickman and McLean (1990). Although *Acremodonta crassicosta* is exceptionally large for a trochaclidid (shell width up to 6.10 mm), it is overshadowed by a probable congener from Wanganella Bank, southern Norfolk Ridge (NZOI sta. P13, 32°10.5'S, 167°21.2'E; 442–449 m). This species is known only by part of a last adult whorl from a shell that must have been at least 9 mm wide. It has much wider spiral cords with correspondingly narrower interspaces than in *A. crassicosta*.

Austrotrochaclis Marshall, gen. nov.

Type species: *Austrotrochaclis ponderi* n. sp.; Recent, New South Wales.

Etymology: Southern *Trochaclis* (Latin).

Diagnosis: Shell minute, up to 2.07 µm wide, thin, teleoconch of up to 1.8 rapidly expanding convex whorls, mi-

←

Explanation of Figures 65 to 72

Figures 65–72. Radulae of *Acremodontina* and *Austrotrochaclis* species.

Figures 65–67. *Acremodontina atypica* (Powell, 1937), adult, off Three Kings Islands, northern New Zealand, 206–211 m, NMNZ M.92196. Figure 65. Central, lateral and inner marginal teeth, scale 10 µm. Figure 66. Outer marginal teeth, scale 10 µm. Figure 67. Tips of outermost marginal teeth, scale 5 µm.

Figures 68, 69. *Acremodontina simplex* (Powell, 1937), adult, off Three Kings Islands, northern New Zealand, 173–178 m,

NMNZ M.92199. Figure 68. Width of radula, scale 10 µm. Figure 69. Tips of inner marginal teeth, scale 5 µm.

Figure 70. *Acremodontina poutama* (E. C. Smith, 1962), ex adult paratype, NMNZ M.19424, off Poutama Island, Stewart Island, New Zealand, 55 m, scale 5 µm.

Figures 71, 72. *Austrotrochaclis ponderi* Marshall, gen. & sp. nov., ex adult paratype, off Long Reef, Sydney, New South Wales, 38 m, AMS C.174898. Figure 71. Tips of outermost marginal teeth, scale 5 µm. Figure 72. Tips of inner marginal teeth, scale 2 µm.

nutely umbilicate, fine spiral grooves on first half teleoconch whorl and on inner third of base. Operculum chitinous, thin, multispiral. Central and lateral teeth presumably present (though indistinguishable from marginals in preparation); marginals long and narrow, tip of each tooth deeply split to form two primary branches, one before the other, each branch with terminal fan of fine, repeatedly branched cusps.

Remarks: The type species of *Austrotrochaclis* differs from all other trochaclidids in its more rapidly expanding teleoconch whorls, and in being sculptured with fine spiral grooves on the first teleoconch whorl and on the inner part of the base. It most closely resembles *Acremodontina* species in having a deep primary bifurcation at the tip of each marginal tooth, but differs in that the central and lateral teeth are apparently slender like the marginals, unlike *Acremodontina* species in which the central and lateral teeth are short and laminar.

Austrotrochaclis ponderi Marshall, sp. nov.

(Figures 46, 53–55, 71, 72; Table 13)

Description: Shell turbiniform, up to 2.07 mm wide, slightly broader than high, spire $0.40\text{--}0.51\times$ as high as aperture, thin, chalky white (etched), umbilical chink very small.

Protoconch $230\text{ }\mu\text{m}$ wide, tip of apical fold pinched at inner extremity, apertural rim simple, sculpture unknown (etched).

Teleoconch of up to 1.80 strongly convex, rapidly expanding whorls, end of last whorl descending at maturity. First half whorl and inner third of base with fine spiral grooves, grooves on spire becoming obsolete, elsewhere smooth. Umbilicus narrow, bounded by sharp angulation, invaded by inner lip to form small, shallow, crescentic chink. Aperture subcircular; outer lip thin at rim, slightly thicker within; parietal glaze continuous with inner lip, thin.

Animal unknown (dried).

Radula (Figures 71, 72). Central and lateral teeth not distinguishable in preparation, apparently slender like marginals. Teeth numerous, very slender, shafts laterally compressed, tip of each deeply split from side to side to form two primary branches, each of which has a curved terminal fan of slender, repeatedly divided cusps. Frontal branch shorter and its terminal fan narrower and with fewer cusps than rear branch, cusps overhanging angulate projection at innermost edge of tooth. Outermost four marginals on each side with shafts fused from based to about mid-length, cusps very slender, deeply and repeatedly branched.

Type data: Holotype AMS C.154371 (2.00×2.10 mm, 1.8 teleoconch whorls) and 2 paratypes (1 AMS, 1 NMNZ): Off Long Reef, Sydney, New South Wales, alive amongst

sponges (identity unspecified), 38 m, 28 May 1972, Shelf Benthic Survey.

Distribution: Off Long Reef, Sydney, New South Wales, Australia, 38 m, living amongst sponges.

Remarks: *Austrotrochaclis ponderi* is distinctive in its low spire, rapidly expanding teleoconch whorls, and teleoconch sculpture of spiral lirae on the first whorl and inner base.

Etymology: After Dr. Winston F. Ponder (AMS).

ACKNOWLEDGMENTS

For the loan of material I am grateful to P. Bouchet (MNHN), S. Hain (Alfred-Wegener-Institut für Polar- und Meeresforschung, Bremerhaven), P. A. Maxwell (Waimate, formerly NZGS), I. Loch and W. F. Ponder (AMS), and A. Warén (Swedish Museum of Natural History, Stockholm). For comments on the manuscript I am grateful to J. H. McLean (Los Angeles County Museum of Natural History), W. F. Ponder (Australian Museum, Sydney), and A. Warén. Thanks to W. St. George (NZGS) for access to the scanning electron microscope, M. Hall for photographic printing, and L. Ratapu for word processing.

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New Zealand Opisthobranchs Associated with the Low Intertidal, Crustose Green Alga *Codium convolutum*: Ascoglossans "Down Under"

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Abstract. Mollusks associate with crustose green algae on many temperate-zone rocky shores. From September 1992 to August 1993, I examined molluscan grazers on the low intertidal, crustose green alga *Codium convolutum*, endemic to rocky shores of northern New Zealand. In spring and fall surveys, grazers were not particularly abundant on the alga at most sites in the Hauraki Gulf (overall < 2 mollusks per algal thallus). The polyphagous turbinid snail *Turbo smaragdus* Gmelin, 1791, was the most common species on *C. convolutum*, but the snail rarely consumed the alga. Ascoglossan (= saccoglossan) opisthobranchs were also abundant: the stenophagous herbivore *Placida dendritica* (Alder & Hancock, 1843) occurred on the alga at Milford Beach (near Auckland) in summer and winter, whereas *Elysia maoria* Powell, 1937, occurred in spring and fall. Both species associated with large, rugose thalli of *C. convolutum*, occurring primarily on the lower surface of thalli where the algal crusts were partially detached from the rocky substratum. Although the mechanisms contributing to this behavior were not fully elucidated, an apparent trophic benefit exists: *Codium* utricles (tips of interwoven siphons on which ascoglossans feed) were substantially larger on the lower surface of *C. convolutum* thalli than on the upper surface. Furthermore, *P. dendritica* was substantially larger on *C. convolutum* than on congeneric algae, with smaller utricles, on other temperate-zone shores.

INTRODUCTION

Green algal species belonging to the genus *Codium* occur on rocky shores throughout the world (Silva, 1962). The genus *Codium* contains over 100 species and exhibits a wide range of morphological forms from prostrate crusts to upright, dichotomously branching thalli (Silva, 1962, 1992). Despite the abundance and diversity of *Codium*, little ecological information is available for most of the species, particularly regarding interactions with molluscan grazers. A variety of chitons and shelled gastropods feed on *Codium* spp. (Dellow, 1953; Santelices et al., 1981), and several genera of ascoglossan opisthobranchs have highly specialized associations with *Codium* spp. (Macnae, 1954; Clark, 1975; Jensen, 1980, 1989, 1993; Brandley, 1984; Trowbridge, 1991a; references therein). Past work on *Codium*-mollusk interactions has focused (1) on asco-

glossan kleptoplasty (reviewed by Clark et al., 1990), stenophagy (Jensen, 1989; Trowbridge, 1991a), and population dynamics (Clark, 1975; Brandley, 1984; Trowbridge, 1992b; references therein), and (2) on the ecological consequences of mollusk feeding (Clark, 1975; Santelices et al., 1981; Trowbridge, 1991b, 1992a, 1993a).

Encrusting species of *Codium* occur on many rocky shores (Table 1) and stenophagous ascoglossans occur and feed on at least five of these species (*C. setchellii*, *C. convolutum*, *C. dimorphum*, *C. stephensiae*, *C. adhaerens*; Macnae, 1954; Willan & Morton, 1984; Trowbridge, 1992a, 1992b; references therein). Malacologists, however, have often overlooked this algal diversity either by not reporting the species (e.g., Thompson, 1973) or by considering crustose *Codium* to be *C. adhaerens* (which is "strictly European in distribution," Silva & Womersley, 1956), irrespective of its geographic location (e.g., Bleakney, 1989).

Because of the high algal diversity, we have the opportunity to compare molluscan assemblages associated with "ecologically equivalent" algal species in different geographic regions. In Chile, the experimental exclusion of

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chitons and gastropods enabled *C. dimorphum* to occupy significantly more intertidal rocky substratum than the alga could in the presence of grazers (Santelices et al., 1981). Grazers were particularly important in reducing algal cover when the alga was desiccation-stressed in summer. In Oregon, USA, the small prosobranch *Lacuna* sp. and the ascoglossan opisthobranch *Placida dendritica* (Alder & Hancock, 1843) numerically dominated the herbivore assemblage on the low intertidal *C. setchellii* (Trowbridge, 1992a). Ascoglossans formed feeding aggregations in surface depressions of the algal crusts, and ascoglossan herbivory during spring and summer appeared to restrict the alga's distribution (Trowbridge, 1991b, 1992a).

To examine the generality of patterns observed in Oregon and Chile, I investigated the molluscan grazers associated with *Codium convolutum* (Dellow) Silva, an encrusting alga endemic to the North Island of New Zealand (previously known as *C. adhaerens* var. *convolutum* before Silva, 1962). The alga occurs on the shore between MLWN and MLWS; its precise tidal level varies with wave exposure and extent of shading (Dellow, 1953). I selected this geographic region and *Codium* sp. for several reasons: (1) Molluscan grazers are abundant and diverse on northeastern New Zealand rocky shores, and many grazers strongly influence macroalgal distribution and abundance (Walsby & Morton, 1982; Creese, 1988). (2) Two species of ascoglossans feed selectively on *Codium* spp. in New Zealand and occur on *C. convolutum* in the Hauraki Gulf region (Reid, 1964; Willan & Morton, 1984; Bleakney, 1989): *Placida dendritica* (referred to as *P. aoteana* (Powell, 1937) before Bleakney, 1989) and *Elysia maoria* Powell, 1937. (3) Some ecological information is available for *C. convolutum* within the Hauraki Gulf (Dellow, 1952, 1953).

I address four questions in this paper: (1) How abundant are mollusks on the encrusting green alga *Codium convolutum* on northeastern New Zealand rocky shores? (2) How widely distributed are ascoglossan opisthobranchs on the alga within the Hauraki Gulf and how abundant are their populations seasonally at a single site? (3) Under what conditions do ascoglossans occur (and presumably feed) on algal thalli? (4) Are the phenology and maximum size of *Placida dendritica* in New Zealand similar to those in other geographic regions?

MATERIALS AND METHODS

In September and October 1992 (spring) and March 1993 (fall), I surveyed 13 rocky sites in the Hauraki Gulf between Leigh and Auckland (Figure 1) on the North Island of New Zealand. At each site, I searched low intertidal rocky substratum for 0.5 to 2 hr to locate *Codium convolutum*. For each crustose thallus encountered, I measured and averaged two diameters (maximum diameter and one perpendicular to it) and categorized surface rugosity on a relative scale from 0 (smooth) to 3 (highly folded and convoluted) (Figure 2). Thallus rugosity presumably is a result of the growth pattern of the alga. When a thallus

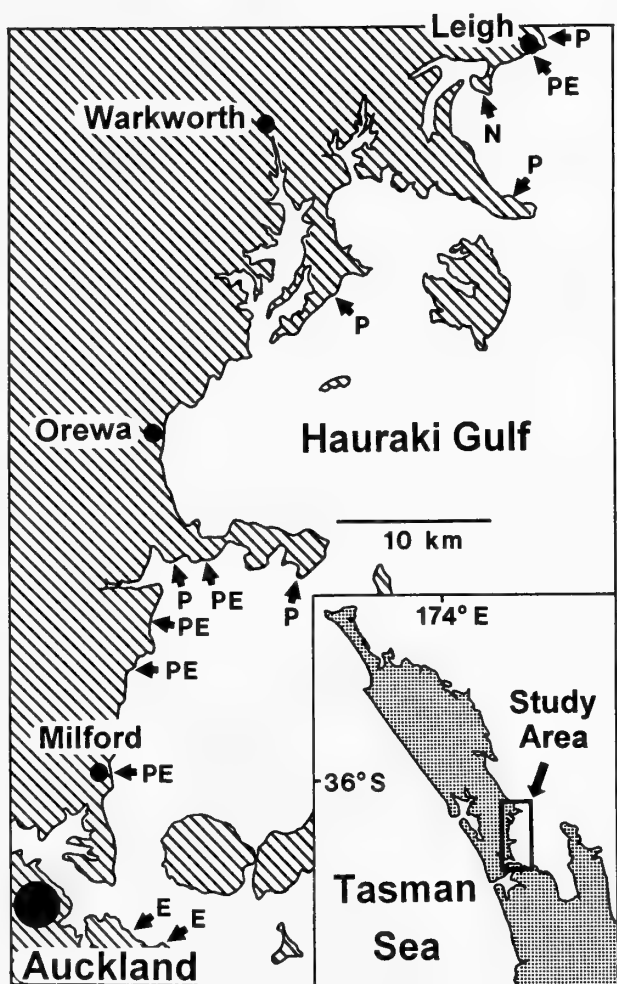


Figure 1

Location of 13 study sites in the Hauraki Gulf, northeastern New Zealand. Symbols denote the occurrence of *Placida dendritica* (P), *Elysia maoria* (E), or neither species (N) based on surveys during September and October 1992 and March 1993.

is small, the entire lower surface is attached to the substratum with rhizoids; as the thallus grows, the expanding areas are forced to buckle up in spots (Figure 2). Partial detachment has been alluded to for other crustose species of *Codium* (Silva, 1959; Trowbridge, 1992a).

During the surveys, I noted all mollusks on the crustose alga. A more detailed sampling was conducted at Milford Beach—monthly surveys from September 1992 to August 1993. I recorded the presence of the ascoglossan *Placida dendritica* on each thallus, but not the number, due to the animal's small size and tendency to burrow under the algal thalli (Figure 2). For all other species, I counted the mollusks found on or under *C. convolutum*. To determine the size-frequency distribution and maximum size of *P. dendritica*, I collected 196 individuals in September (spring), May (fall), and July (winter). I gently blotted each slug

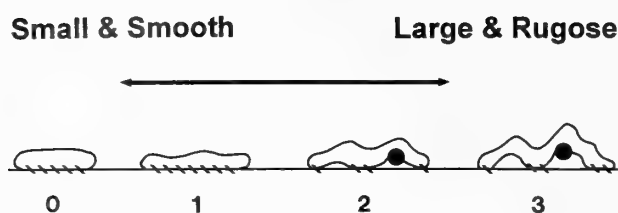


Figure 2

Schematic diagrams of thallus rugosity categories (0 to 3) of the crustose green alga *Codium convolutum* (cross sections through thalli). Rhizoidal attachments are indicated by slashed lines. Black circles indicate the thallus location where most ascoglossans were found during this study.

on paper towels, then weighed it to the nearest 0.1 mg. The blotting and weighing error for *P. dendritica* was 2.7% (Trowbridge, 1989). Size data for *Elysia maoria* in the Hauraki Gulf are already available (Reid, 1964).

Because ascoglossans are suctorial feeders that puncture their algal hosts and suck out the cytoplasm, the diameter of the utricles (cortical tips of interwoven filaments forming *Codium* thalli) may restrict feeding. For example, Macnae (1954) noted that there was a positive correlation between size of *Placida dendritica* (as *Hermatea capensis* Macnae, 1954) and utricle diameter. To quantify utricle size-distribution of *C. convolutum*, I examined algal thalli under a dissecting microscope and measured the diameter of 25 utricles from the top surface of 10 thalli and 15 utricles from the lower surface of five of these thalli. To avoid bias in selecting utricles, I started in the center of the microscopic field and measured the first 25 (or 15) utricles in series that intercepted the ocular micrometer. I measured fewer utricles from the lower surface because they were less common, forming only where the alga was no longer attached to the substrate (Figure 2).

Sea surface temperature (SST) and surge height data were obtained from the Leigh Marine Laboratory climatic monitoring program (courtesy of Jo Evans). Both values were measured every morning on the shore at Leigh. Water temperature was determined daily for a bucket of seawater collected from the sea surface at ~ 9:30 a.m. Surge height was determined visually from a set of markers attached to an inclined rocky surface at 0.2 m intervals (vertical height). The climatic observer noted the highest and lowest point reached by the sea surface over a 3 min period; the difference between the two values represented surge height.

RESULTS

Codium convolutum

The encrusting green alga occurred on three different types of low intertidal rocky substrate: vertical or steeply sloping rocky faces, sides of large boulders, and gently sloping rocky benches. The alga was most abundant in the first two types of environments with the alga locally cov-

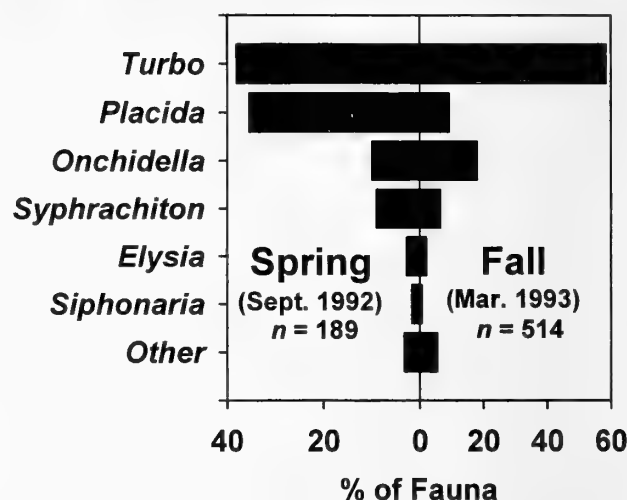


Figure 3

Molluscan assemblages on the crustose green alga *Codium convolutum* at several sites in the Hauraki Gulf in spring and fall. Sample sizes indicate total number of mollusks found in each season.

ering close to 100% of the primary cover and growing tightly adherent to the rocky substrate. In contrast, the alga was patchily distributed on sloping rocky benches, with few thalli at many sites and extensive populations at other sites (e.g., Milford Beach). Thallus diameter ranged from 0.8 to 82.7 cm; the majority of thalli were < 15 cm in diameter. *Codium convolutum* was relatively smooth (rugosity of 0 to 1) when < 5 cm, but surface rugosity increased significantly with thallus size (Kruskal Wallis, $H = 165.3$, $P < 0.001$, $n = 288$ thalli).

Molluscan Assemblage

A diversity of mollusks associated with *Codium convolutum* in the Hauraki Gulf, including the turbinid cat's eye snail *Turbo smaragdus* Gmelin, 1791; ascoglossan opisthobranchs *Placida dendritica* and *Elysia maoria*; pulmonates *Onchidella nigricans* (Quoy & Gaimard, 1832) and *Siphonaria zelandica* Quoy & Gaimard, 1833; and the chiton *Syphrachiton pelliserpentis* (Quoy & Gaimard, 1835) (Figure 3). Pulmonates and chitons were most common on large expanses of *C. convolutum* on shady, steep rocky surfaces, whereas prosobranch snails and opisthobranchs were most common on thalli on gently sloping rocky benches. Data pooled from all sites showed that herbivore abundance was low. For example, during the spring survey, 189 mollusks were noted on 335 thalli (0.6 mollusks per thallus); during the fall survey, the overall value was 1.9 mollusks per thallus. The polyphagous *T. smaragdus* was the most common mollusk (Figure 3). Yet, in the laboratory, *T. smaragdus* would not eat *C. convolutum*, and evidence of snail grazing was extremely uncommon on the shore and was limited to cases of desiccation-stressed thalli.

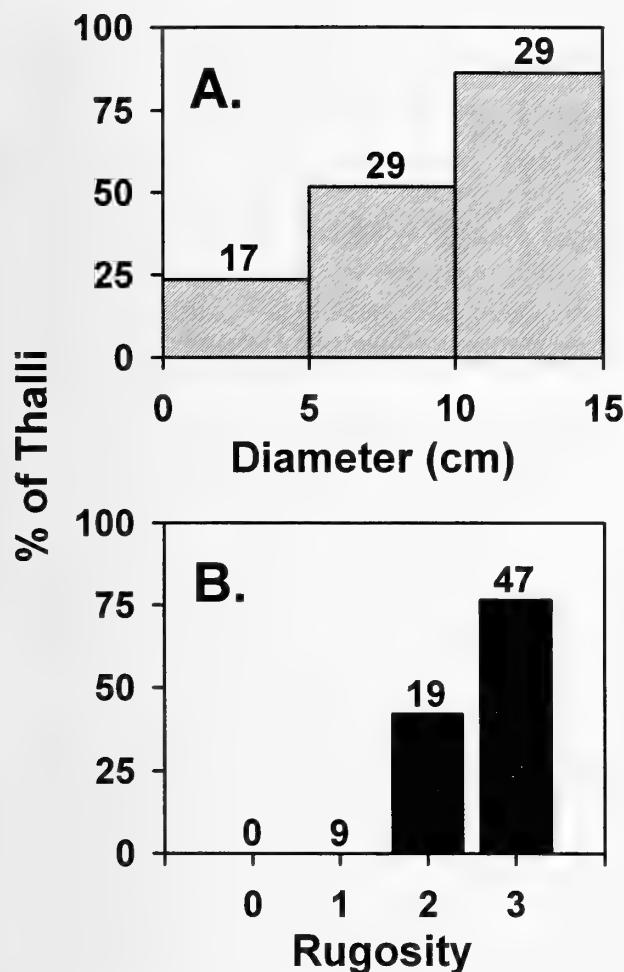


Figure 4

Frequency of occurrence of *Placida dendritica* on *Codium convolutum* based on (A) algal thallus diameter and (B) surface rugosity. Numbers above each bar denote the number of algal thalli examined in each size class or rugosity category. Data were collected from Milford Beach in September 1992; no small, smooth thalli (rugosity = 0) were observed in this particular census.

Either the snail was not feeding, or it was feeding on the lush microalgae covering the crustose alga's surface.

Ascoglossan Opisthobranchs

Ascoglossans were widely distributed on the western shore of the Hauraki Gulf (Figure 1): *Placida dendritica* occurred at 10 of the 13 sites surveyed, and *Elysia maoria* occurred at seven sites. Ascoglossans composed 38.2% of the molluscan assemblage in spring and 11.3% in fall (Figure 3). Both *P. dendritica* and *E. maoria* were most common at Milford Beach and occurred significantly more frequently on large than on small algal thalli (G -test, $G = 19.7$, $df = 2$, $P < 0.001$, $n = 75$). For example, in September 1992, *P. dendritica* occurred on 86% of thalli > 10

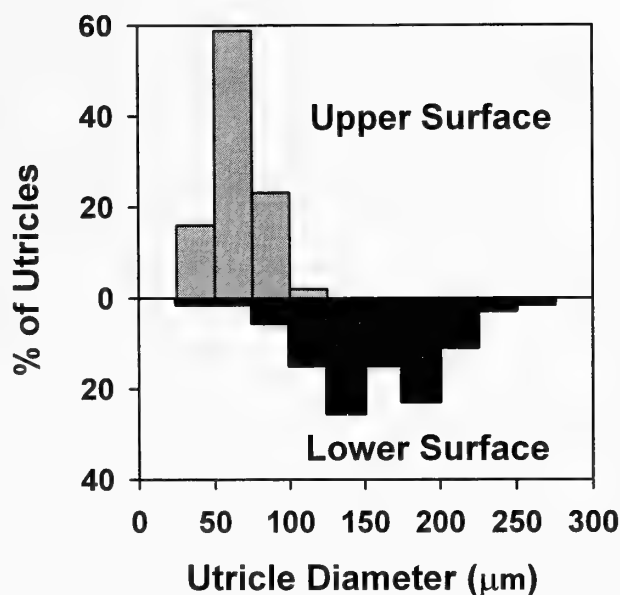


Figure 5

Size-frequency distributions of utricles on the upper and lower thallus surface of *Codium convolutum*. Data in top panel based on 25 utricles from each of 10 thalli; data in bottom panel based on 15 utricles from each of five thalli.

cm in diameter and on 24% of thalli ≤ 5 cm (Figure 4A). Furthermore, the frequency of ascoglossan occurrence increased significantly with increased rugosity of the algal host (Figure 4B, $G = 24.7$, $df = 2$, $P < 0.001$, $n = 75$).

Ascoglossans occurred almost exclusively on the lower surface of *Codium convolutum* where the algal crust pulled away from the rocky substratum (Figure 2), creating protected chambers that may offer refuge from desiccation and/or predators. The presence of *Placida dendritica* and *Elysia maoria* was clearly apparent (despite their cryptic location and coloration) due to slime trails and often white egg masses in algal crevices and under loose edges. Although the cause for the ascoglossans' secretive habit was not explicitly examined, the size range of algal utricles (cortical structures that ascoglossans puncture to feed on *Codium*) differed markedly on the alga's upper and lower surfaces (Figure 5). Utricles on the upper surface were mostly $< 100 \mu\text{m}$ ($\bar{x} = 74 \mu\text{m}$), whereas those on the lower surface were mostly $> 100 \mu\text{m}$ diameter ($\bar{x} = 161 \mu\text{m}$).

The seasonality of the ascoglossans was rather unusual (Figure 6A). *Placida dendritica* was most common in summer (January) and winter (August) when sea surface temperature (Figure 6B) was at an annual high ($\sim 20^\circ\text{C}$) and an annual low ($\sim 13^\circ\text{C}$), respectively. During each of these seasonal peaks, the species occupied $\sim 60\%$ of the algal thalli sampled. In contrast, *Elysia maoria* occurred in the Hauraki Gulf primarily in the spring (November) and fall (April) with peak occurrence at 10% of the thalli. The phenology of the two species was unrelated to temporal

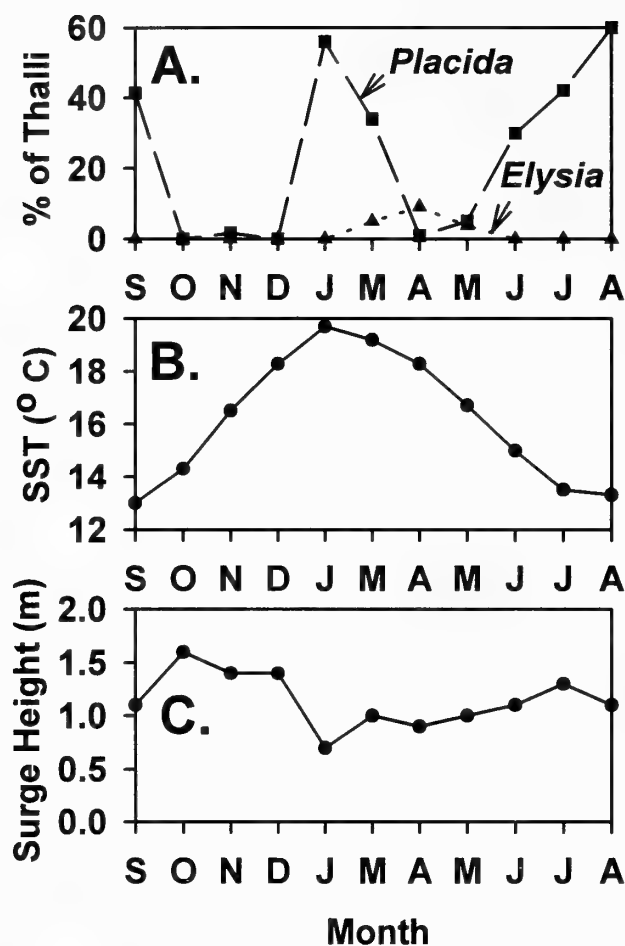


Figure 6

(A) Seasonal occurrence of two species of ascoglossans on *Codium convolutum* at Milford Beach near Auckland. Data expressed as percent of algal thalli surveyed. Sample sizes ranged from 50 to 130 thalli examined per month. (B) Sea surface temperature (SST) and (C) surge height measured at Leigh.

changes in sea surface temperature (SST) or wave surge height (Figure 6B, C).

Placida dendritica also exhibited two other important features in northeastern New Zealand: (1) the species generally did not aggregate on *Codium* hosts, and (2) many animals grew quite large. Although most individuals were < 10 mg, *P. dendritica* reached wet weights of 20 mg (corresponding to body lengths of ~15 mm) on *C. convolutum* (Figure 7). Maximum body size was largest in the spring collection (September) when SST was 13.6°C. Although only three collections of slugs were made, maximum size was not clearly temperate-dependent (Figure 7).

DISCUSSION

Molluscan Assemblage

Mollusk-*Codium* associations vary considerably among geographic regions (Chile, Oregon, New Zealand). These

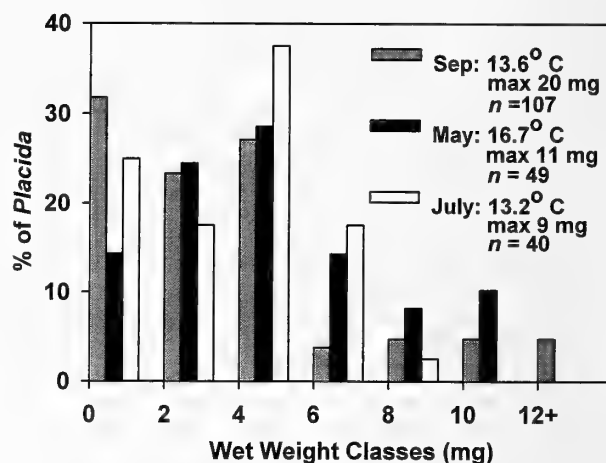


Figure 7

Wet weight (mg) of *Placida dendritica* collected from *Codium convolutum* in the Hauraki Gulf in September 1992 (spring), May 1993 (fall), and July 1993 (winter). SST on the days of slug collection are indicated. Sample size and maximum ascoglossan weight are denoted for each collection.

differences are due in part to regional differences in species composition and ecological interactions. For example, the scarcity of large herbivorous snails, *Tegula funebris* Adams, 1855, in the northeastern Pacific low intertidal zone is related to seastar predation (Paine, 1969). The small prosobranch *Lacuna* sp., however, is extremely abundant on Oregon shores (Trowbridge, 1992a). There are no comparable seastar species in the Hauraki Gulf, and large intertidal snails are common (reviewed by Creese, 1988). *Turbo smaragdus* is abundant but rarely damages intertidal *C. convolutum* (but see Dellow, 1953). In Chile, however, the large snail *Tegula atra* (Lesson, 1830) is one of several grazers that consumes *C. dimorphum* (Santelices et al., 1981). Another intriguing geographic difference is the abundance of pulmonate mollusks that may eat *C. dimorphum* in Chile (Santelices et al., 1981) and *C. convolutum* in New Zealand (Figure 3) but not *C. setchellii* in Oregon (Trowbridge, 1992a). *Onchidella borealis* Dall, 1871, is common on red algal turfs on shady, mid intertidal vertical walls in Oregon but not on the crustose *C. setchellii* on more exposed, low intertidal benches (Trowbridge, 1992a; personal observation).

The scarcity of some mollusks on crustose species of *Codium* is related in part to two types of physical disturbance: sand scour and wave action. *C. setchellii* in Oregon occurs most abundantly on sand-scoured benches (Trowbridge, 1992a). Large benthic grazers are often excluded by sand inundations, whereas small grazers such as *Placida dendritica* and *Lacuna* sp. rapidly settle during periods of low sand movement (Trowbridge, 1992a, 1992b). At Milford Beach and similar sites in the Hauraki Gulf that are periodically inundated with sand, siphonarians, chitons, and limpets do not commonly associate with low intertidal *C. convolutum*. On steep rocky walls or boulders, such

grazers are abundant on and around the alga. There are also striking differences in wave action; sites in the Hauraki Gulf experience little wave action (mean monthly surge height was < 2 m; Figure 6C), whereas Chilean and Oregon sites with crustose *Codium* (Santelices et al., 1981; Trowbridge, 1992a, 1992b) are on wave-swept shores.

Ascoglossan Opisthobranchs

Phenology: The phenology of New Zealand ascoglossans (Figure 6) is strikingly different from that of species reported on other shores. Reid (1964) reported that *Elysia maoria* was present all year on rocky shores close to Auckland (though she pooled data from different sites). Although I also found *E. maoria* at different sites in many months of the year, when I focused on an individual site (Milford Beach) and recorded ascoglossan abundance, detectable populations were only present in spring and fall. Surveys of a congeneric, upright branching alga, *Codium fragile* subsp. *tomentosoides*, in the Hauraki Gulf indicated a similar phenology of *E. maoria* (Trowbridge, unpublished data). Although *E. maoria* also occurs in southern Australia (Thompson, 1973), its phenology and demography are largely unknown on those shores.

Placida dendritica is typically abundant on cold-water shores in spring and summer and on warm-water shores primarily in winter (summarized by Trowbridge, 1992b). Given the seasonal range of water temperature in the Hauraki Gulf (Figure 8), I expected to see the species only in winter, not in summer and winter. *P. dendritica* may also exhibit a bimodal seasonality on South African shores, because Macnae (1954) reported collecting the species (as *Hermaea capensis*) in July, December, and January. On most shores, however, the species has a unimodal seasonality. The most plausible explanation for these phenological differences in geographically distant regions is different seasonal temperature ranges (Figure 8). During this study, the early spring (1992) and following winter (1993) were characterized by unusually low water temperatures in northeastern New Zealand. Yet, water temperatures were still substantially higher than those in many other parts of the geographic range of *P. dendritica* (Figure 8). Discrete warm water masses could have brought competent larvae of *P. dendritica* to Hauraki Gulf shores in winter, and cold water masses could have brought larvae in summer. Daily temperature records (as opposed to monthly means shown in Figure 6B), however, indicate no such oceanographic phenomenon occurring.

Several other processes could produce the observed bimodal seasonality: (1) Two thermally distinct ecotypes of the ascoglossan species may occur in northeastern New Zealand. (2) Summer and winter populations may represent slugs that are physiologically acclimated to different temperatures. Clark (1975) reported that the thermal tolerance of *Placida dendritica* was related to ambient temperature: individuals from cold water had a lower thermal tolerance than conspecifics collected from the same region

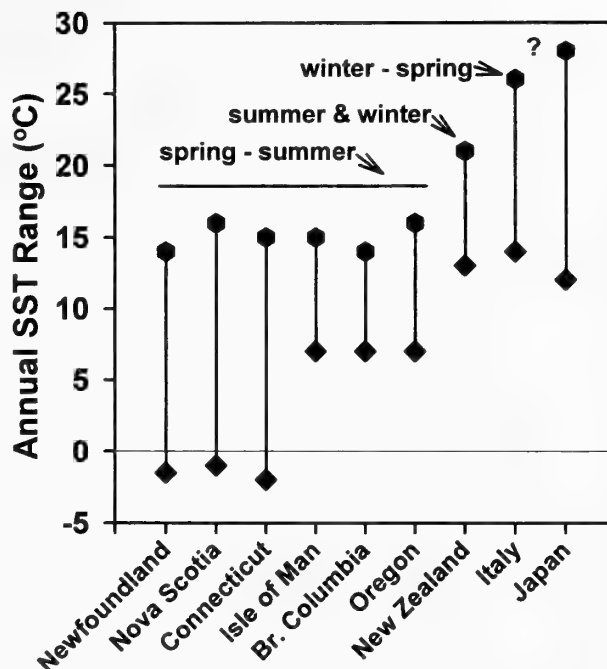


Figure 8

Annual temperature range in regions where *Placida dendritica* has been studied. The seasons of ascoglossan occurrence are indicated. ? denotes detailed phenological data are not available. Data are from Miller, 1961; Schmekel, 1968; Clark, 1975; Bleakney, 1989; Cayan et al., 1991.

in summer. (3) Larval recruitment may be continuous, but the presence of ascoglossan populations on algal hosts may represent periods in which planktonic and/or benthic predators did not prevent ascoglossan establishment. (4) Local factors or random events may also have produced the observed seasonal patterns.

Because the larvae of both ascoglossan species are planktotrophic (Reid, 1964; Clark, 1975), they probably spend considerable time in nearshore currents. In Oregon, the southward-moving current brings larvae from northern localities with source populations of *Placida dendritica*. In New Zealand, however, the current moves southward along the northeastern shoreline (Morton & Miller, 1968), and there are no upcurrent, temperate-zone land masses. Thus, the Hauraki Gulf may be recruitment limited. When I transplanted *Codium fragile* in mesh bags for one month near the Leigh Marine Laboratory, ascoglossan recruitment was 1000-fold less than occurred in comparable transplants on the Oregon coast (Trowbridge, 1992b and unpublished data).

Abundance: At Milford Beach, peak occurrence of *Placida dendritica* was 60% of the algal thalli (Figure 6A), but peak abundance was 5–10 slugs per thallus (personal observation). At Strawberry Hill, Oregon, 32% of the *Codium setchellii* thalli were occupied by *P. den-*

Table 1.

Encrusting species of *Codium* throughout the world and the "typical" range of diameters of the utricles (cortical tips of interwoven filaments forming the algal thallus) (Dellow, 1952; Silva, 1951, 1959, 1960, 1962; Silva & Womersley, 1956; Ricker, 1987; Burrows, 1991). Extreme minimum and maximum utricule diameters are enclosed in parentheses.

<i>Codium</i> spp.	Geographic region	Range of utricule diameters (μm)
<i>setchellii</i>	N.E. Pacific	(45-)65-90(-125)
<i>hubbsii</i>	southern California, Baja & Japan	60-140(-220)
<i>convolutum</i>	northern New Zealand	28-100(-200*)
<i>dimorphum</i>	southern New Zealand, Tasmania & Chile	(47-)55-80(-90)
<i>arabicum</i>	tropical Indo-Pacific	(50-)60-105(-125)
<i>capitulatum</i>	southern Australia	40-140
<i>lucasii</i>	southern Australia & South Africa	(45-)50-105(-130)
<i>stephensiae</i>	South Africa	55-110(-125)
<i>adhaerens</i>	N.E. Atlantic	40-100
<i>effusum</i>	N.E. Atlantic, Mediterranean & Adriatic Sea	150-300(-450)
<i>intertextum</i>	S.W. Atlantic, Caribbean & Canary Islands	(45-)70-110(-215)
<i>subantarcticum</i>	southern South America, Falkland Islands & Macquarie Island	120-350

* 262 μm in this study.

dritica (Trowbridge, 1992a). Peak occurrence was > 50% of the thalli surveyed, and peak abundance was 72 to 100 animals per thallus (Trowbridge, 1991a, and unpublished data). Several hypotheses may explain such geographic variation in ascoglossan abundance including increased recruitment, decreased predation, and increased productivity with increased latitude (Clark & DeFreese, 1987; Trowbridge, 1993b). The first hypothesis appears to be supported (higher recruitment in Oregon at 44°N than in New Zealand at 36-37°S), but little information is available to evaluate the other two hypotheses for this particular ascoglossan-algal interaction.

Large, highly rugose thalli of *Codium convolutum* were attacked by ascoglossans significantly more frequently than smaller, less rugose thalli (Figure 4). Trowbridge (1992a) reported a comparable size-specific pattern for *C. setchellii* with one crucial difference. In Oregon, ascoglossans occurred in the exposed surface depressions of the algal crust; large, highly folded thalli thus provided more slug habitat than small, smooth thalli (Trowbridge, 1992a). In New Zealand, however, *Placida dendritica* occurred primarily underneath *C. convolutum* where the algal crusts buckled up from the rocky substratum (Figure 2).

The factors contributing to this cryptic behavior were not fully examined but may include slugs (1) minimizing desiccation stress, (2) avoiding predators, or (3) seeking large utricles. Although avoidance of desiccation stress seems intuitively obvious, my observations did not support this hypothesis. Because of the alga's low intertidal location, it is not exposed during low tide every day. When I observed thalli as they became exposed on ebbing tides, slugs were not on the top of algal crusts

and slime trails did not often cross the surface. Thus, the species was not hiding in direct response to aerial exposure. Furthermore, slugs attacked *Codium* thalli at the upper end of the alga's tidal range significantly more frequently than thalli lower on the shore (Trowbridge, unpublished data); this result supported the observation that on Oregon shores *Placida dendritica* attacked *C. setchellii* at the upper end of its tidal range more frequently than conspecific thalli at the lower end of its range (Trowbridge, 1989).

The geographic variation in location of slugs on *Codium* crusts may reflect differential predation patterns due to differences in the abundance and/or species composition of the predator assemblages in different regions. The importance of predation, however, on temperate and boreal species of ascoglossans has only begun to be explored (Trowbridge, 1994). Finally, the location of the ascoglossans may reflect food availability. *C. convolutum* has cortical patches of utricles on the lower surface. The South African *C. stephensiae* is one of the few other species of crustose *Codium* that has a "ventral" cortex of utricles (Silva, 1959). Thus, *Placida dendritica* should occur on the upper surface of most species of crustose *Codium*; on South African and northern New Zealand shores, the slugs may occur on the upper and/or lower surfaces.

Body Size: Another geographic difference is ascoglossan size. *Placida dendritica* in Oregon grows to ~ 5 mm or ~ 5 mg on encrusting *Codium setchellii* (Trowbridge, 1992b). In contrast, on *C. convolutum* the ascoglossan grew 2-3 times larger and ~ 4 times heavier. If *P. dendritica* is a single cosmopolitan species (as suggested by Bleakney, 1989), geographic differences in asco-

glossan body size may reflect differences in algal food species and/or water temperature. Although large differences in body size have been reported for *P. dendritica* feeding on *Codium* versus *Bryopsis* (e.g., Trowbridge, 1992b), comparable size differences for conspecifics feeding on different *Codium* species (at similar or different water temperatures) have not previously been explored.

Crustose *Codium* species differ in at least two important ways: the size and wall thickness of algal utricles. Maximum utricle size (Table 1) was much greater for the New Zealand *C. convolutum* (262 μm , this study) than for the Oregon *C. setchellii* (125 μm). Observations by Macnae (1954) and Jensen (1975, 1981) indicate that algal utricle diameter (or filament width) restricted which ascoglossans could feed; small individuals could feed only on algal species with small utricles or narrow filaments, whereas large individuals fed on algae with larger utricles or broader filaments. Although Jensen noted that this feeding restriction was not applicable to all ascoglossans, Macnae (1954) noted that it was true for *Placida dendritica* (as *Hermæa capensis*). Therefore, the large range of utricle diameters on *C. convolutum* (28–262 μm) would enable small ascoglossans to feed and larger conspecifics to survive. Based on utricle size-range alone (Table 1), *P. dendritica* should be larger on *C. convolutum* than on its ecological counterparts *C. setchellii*, *C. adhaerens*, and *C. stephensiae*. Although the first prediction is supported, data are not available to evaluate the latter two predictions. Furthermore, *C. convolutum*, *C. hubbsii*, and *C. intertextum* should support the largest individuals of *P. dendritica*.

Some *Codium* species, however, have a thickened apical wall (Figure 9), and thick walls presumably are more difficult for ascoglossans to puncture when feeding than thin walls. If utricle diameter and apical wall thickness are both important determinants of feeding, *Placida dendritica* should grow larger on *C. convolutum* than on other crustose species of *Codium* (Table 1; Figure 9). Also, ascoglossans on *C. dimorphum* and *C. stephensiae* should be small because of small utricles with thick apical walls. To evaluate these predictions, we need quantitative information on ascoglossan-*Codium* associations in previously studied and unstudied regions.

Species Complex: The assumption implicit within the preceding discussion is that *Placida dendritica* is a single, widespread species as suggested by Bleakney (1989). An alternative explanation—that may account for some of the geographic variation in phenology, abundance, and body size—is that *P. dendritica* may represent a complex of sibling species. Two types of evidence support this latter interpretation: (1) Dispersal of a temperate to boreal species across the equatorial region

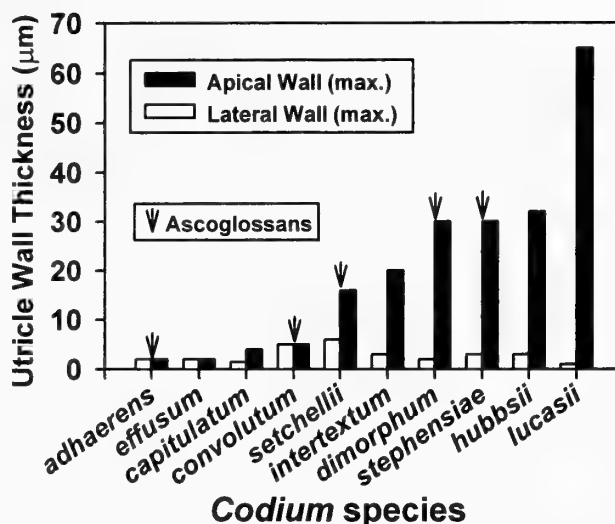


Figure 9

Species-specific differences in wall thickness of *Codium* utricles (cortical tips of interwoven siphons). *Placida dendritica* and *Elysia* spp. have been reported for the five algal species indicated. Data based on Dellow, 1952; Silva, 1951, 1959, 1960, 1962; Silva & Womersley, 1956; and Burrows, 1991.

seems unlikely given the barrier of warm temperatures and ocean currents. (2) *P. dendritica* was originally described in New Zealand and in South Africa as distinct from the northern species. Although Bleakney (1989) found no significant differences in radular or penial structure between northern and southern hemispheric populations of *P. dendritica*, considerable morphological variation does exist in external body features (e.g., number and shape of cerata) between Oregon and New Zealand populations (Trowbridge, unpublished data). Despite the taxonomic uncertainty, however, geographic comparisons of phenology and demography of one or several related ascoglossan species provide valuable insight to how herbivore-algal interactions vary on geographically distant shores.

ACKNOWLEDGMENTS

I thank M. Miller, W. Ballantine, G. Boone, and R. Taylor for discussions that significantly improved the research, and H. Ross for valuable assistance in the field and laboratory. J. Evans kindly provided temperature and surge height data from the Leigh Marine Laboratory climatic monitoring program. I thank R. Creese for sponsoring me at the University of Auckland, and A. Rees and A. Cozens for generous advice and support at the Leigh Marine Laboratory. I thank S. Navarrete, B. Roth, and two anonymous reviewers for their constructive comments on earlier drafts of this paper. The research was supported by the Leigh Marine Laboratory, University of Auckland,

and a National Science Foundation grant (INT-9202846) to the author. While preparing this manuscript, I received support from an Andrew Mellon Foundation grant to J. Lubchenco and B. Menge. I thank L. Weber for providing me desk space in his laboratory at the Hatfield Marine Science Center, and S. Gilmont and J. Webster for their valuable and cheerful library assistance.

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Reproductive Cycle of *Glycymeris gigantea* (Reeve, 1843) (Bivalvia: Glycymerididae) in Bahía Concepción, Baja California Sur, Mexico

by

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Abstract. The benthonic community in Bahía Concepción includes the bivalve mollusk *Glycymeris gigantea* (Reeve, 1843), a potential fishery resource. This study provides information concerning the reproductive cycle of this species and its relationship to water temperature. Bimonthly, from October 1988 to August 1990, specimens of the clam *Glycymeris gigantea* were collected at Santispac, Punta Arena, and Punta Amolares, Bahía Concepción, B.C.S. The gonadal development was analyzed using common histological techniques and data on oocyte size frequencies. The developmental phases were classified into five stages: undifferentiated, active, ripe, spawning, and spent. Some degree of spawning was continuous during the study period. Gametogenesis is most active from February to April. The spawning frequency was highest in October, coinciding with highest values of the condition factor (Fc), suggesting some relationship between them. At the same time, a marked decrease of water temperature from 29°C to 19°C occurred. When *Glycymeris gigantea* was compared to other bivalve species in Bahía Concepción, marked differences in the time of the highest period of spawning were observed.

INTRODUCTION

The Indian clam *Glycymeris gigantea* (Reeve, 1843) is a member of the bivalve community of Bahía Concepción, Baja California Sur. Its distribution is recorded from Bahía Magdalena, Baja California Sur, to Acapulco, Guerrero, Mexico, and includes the Gulf of California (Keen, 1971). It is occasionally harvested for its shell, which is used for ornamental purposes. This species is considered to have potential as a fishery (Baquero & Stuardo, 1977). Densities as high as five individuals/m² were recorded by Baquero & Stuardo (1977) for Bahía Concepción. The habitat is sandy bottom at about 15 m depth.

Despite the importance of this clam as a potential fishery, its biology and ecology are not well understood. Muciño & Baquero (*in* Baquero, 1989) determined the gonadal cycle in Bahía Concepción and reported shell growth rates of 5 mm/month. Included in studies of other species

of the genus *Glycymeris*, Lucas (1965) studied the gonadal cycle of *Glycymeris glycymeris* in France.

This research is part of a program to obtain information about the reproductive cycles of the potentially commercially important bivalves in Bahía Concepción, especially the seasons in which they are sexually active, their peak spawning periods, sex ratio, and the seasonal variations of their reproductive condition. These are important variables needed to estimate abundance and recruitment and to determine interspecies relationships. In this study, the reproductive cycle of *Glycymeris gigantea* was investigated through analysis and subjective grading of histological gonad sections and measurement of oocyte sizes.

MATERIALS AND METHODS

Bimonthly, from October 1988 to August 1990, 30 to 60 specimens of *Glycymeris gigantea*, ranging from 35 to 90 mm in length (mean = 65), were collected randomly. Sampling was made by skin diving between 2 to 6 m at Santispac, Punta Arena, and Punta Amolares, Bahía Concepción, B.C.S. (Figure 1). The surface temperature of the water at the time of collection was recorded. The shell

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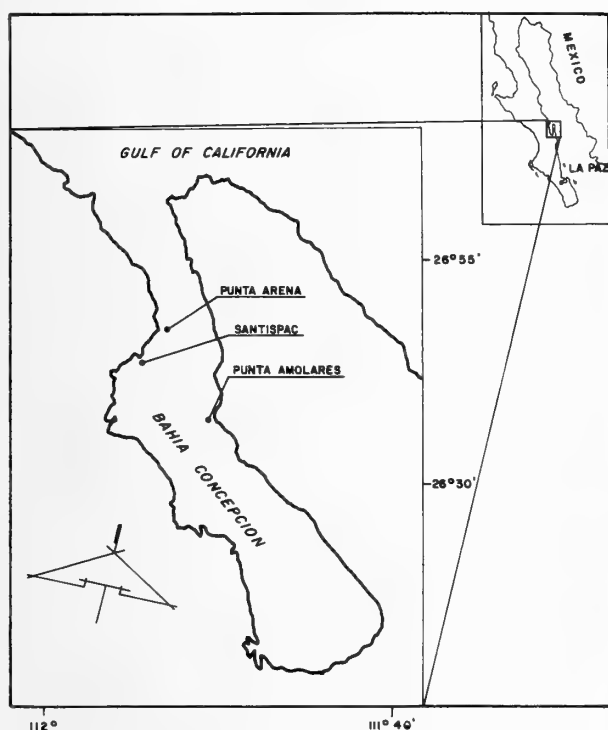


Figure 1

Location of collection sites of *Glycymeris gigantea* in Bahía Concepción, B.C.S. Mexico.

length of all clams was measured to the nearest 0.1 mm using a vernier caliper. The clams were fixed in a neutral solution of 10% formalin prepared with seawater. The shells were removed, and the soft body was weighed.

For histologic studies, a slice of tissue was obtained from the dorsal area of the body of each clam, including the gonad and the foot. This tissue was dehydrated in alcohol and embedded in paraffin (Humason, 1979). Sections (7 μ m) were made and stained with Harris hematoxylin and counterstained with eosin (Humason, 1979). The sex ratio in the population was obtained from histological analysis of all the clams collected, separating the females and the males in the samples and determining the percent of each sex in the study period.

The relative frequency of the gonadal development phases was obtained. They were defined according to the criteria of Baqueiro & Stuardo (1977) into five categories: undifferentiated, active, ripe, spawning (expelling gametes), and spent.

In addition, the diameter of at least 100 oocytes was measured, using an eyepiece graticule calibrated with a stage micrometer, in each of six females selected by sample with a random number table. The measurements were made along the longest axis in the oocytes sectioned through the nucleus. From these data, mean oocyte size and standard deviation were obtained. Individuals with few mea-

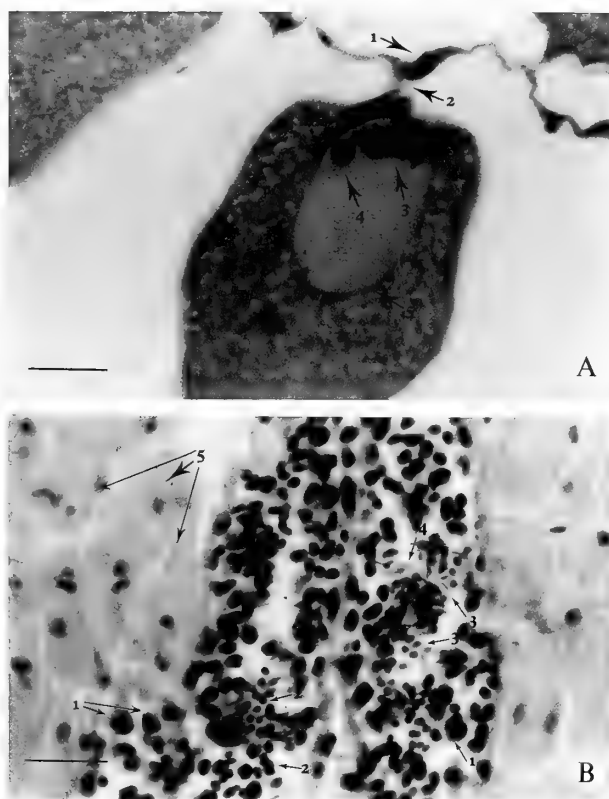


Figure 2

A. Intraovarian ripe oocyte. (1) Follicle cell. (2) Stalk attaching the oocyte with the follicle wall. (3) Chromatin. (4) Nucleoli and (5) Nucleus. Scale = 25 μ m. B. Tubule: (1) Spermatogonia. (2) Spermatocytes. (3) Spermatids. (4) Spermatozoa. (5) Granular fine conjunctive tissue. Scale = 25 μ m.

surable oocytes and extensive phagocytosis were not considered, following the criteria of Grant & Tyler (1983a, b).

The condition factor (Fc) was determined using Fulton's equation (Hile, 1936):

$$Fc = \frac{Wt}{Lt^3}.$$

Where:

Fc is the condition factor.

Wt is the soft body weight in g.

Lt is the shell length in mm.

RESULTS

The sex ratio of specimens sampled during this study was 59% male: 40.5% female: 0.5% hermaphroditic. Both male and female follicles had the same microscopic phases. In February, the smallest sizes (35 to 40 mm) were collected, though for that month the mean was 70 mm. Descriptions of the phases of gonadal development follow:

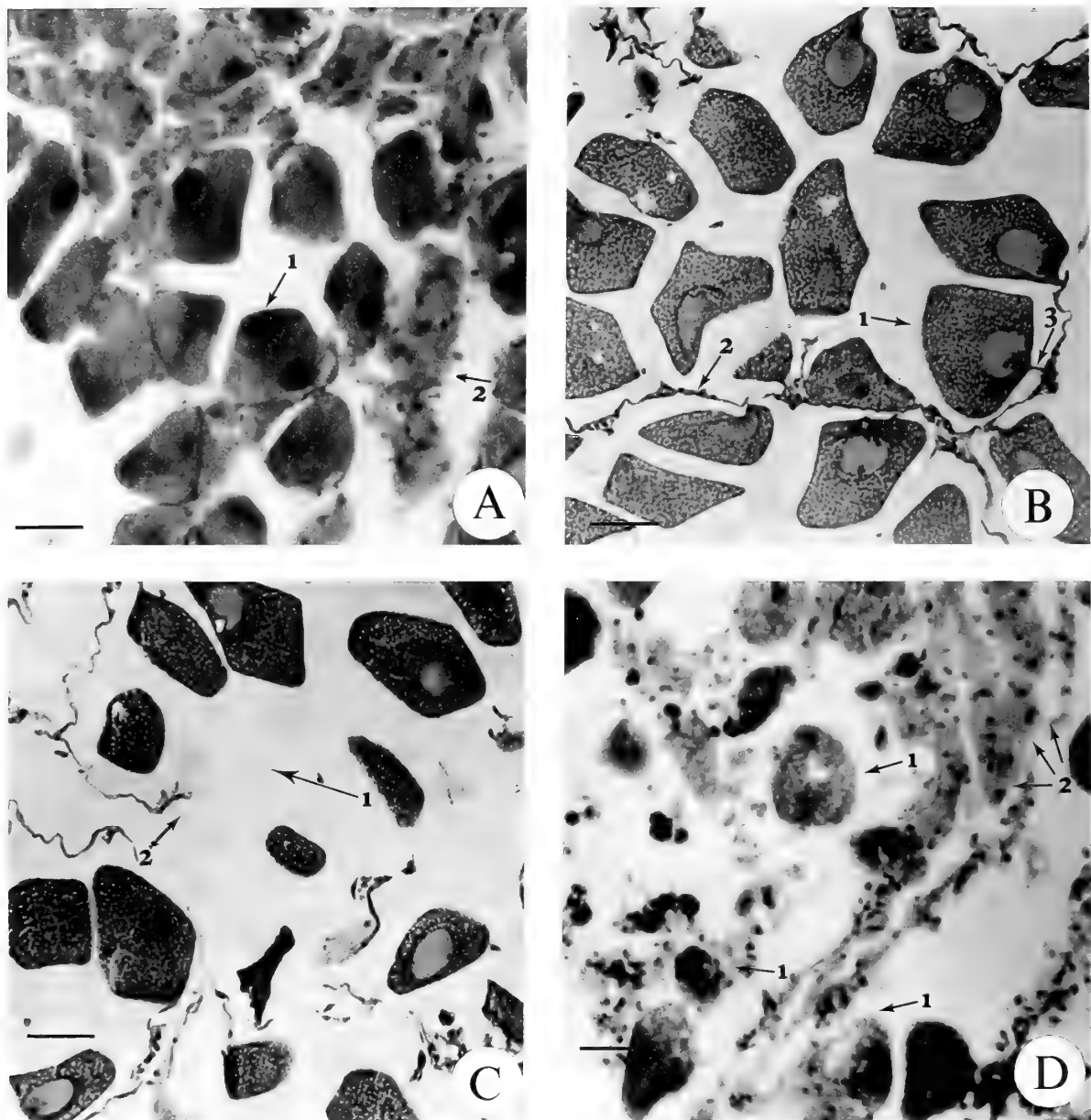


Figure 3

Oogenesis in *Glycymeris gigantea*. A. Active in February: (1) Oocyte in vitellogenesis. (2) Conjunctive tissue. B. Ripe oocyte in October: (1) Ripe oocyte. (2) Follicle wall. (3) Stalk attaching the oocyte with the follicle wall. C. Spawning in October: (1) Space inside the follicle. (2) Broken wall of follicle. D. Spent in December: (1) Oocyte in absorption. (2) Granular fine connective tissue. Scale = 100 μ m.

Developmental Stages

Undifferentiated: This stage is characterized by total absence of follicles and gametes. It is not possible to distinguish the sex. The connective tissue occupies all the space between the follicles.

Females: Active. Follicles are visible. Oocytes inside them increase in size and number. Developing oocytes are attached to the wall of the follicle while they become ripe (Figure 2A). The connective tissue between follicles decreases as gonadic tissue increases, and is formed by cells with fine granulations and pycnotic nuclei (Figure 3A).

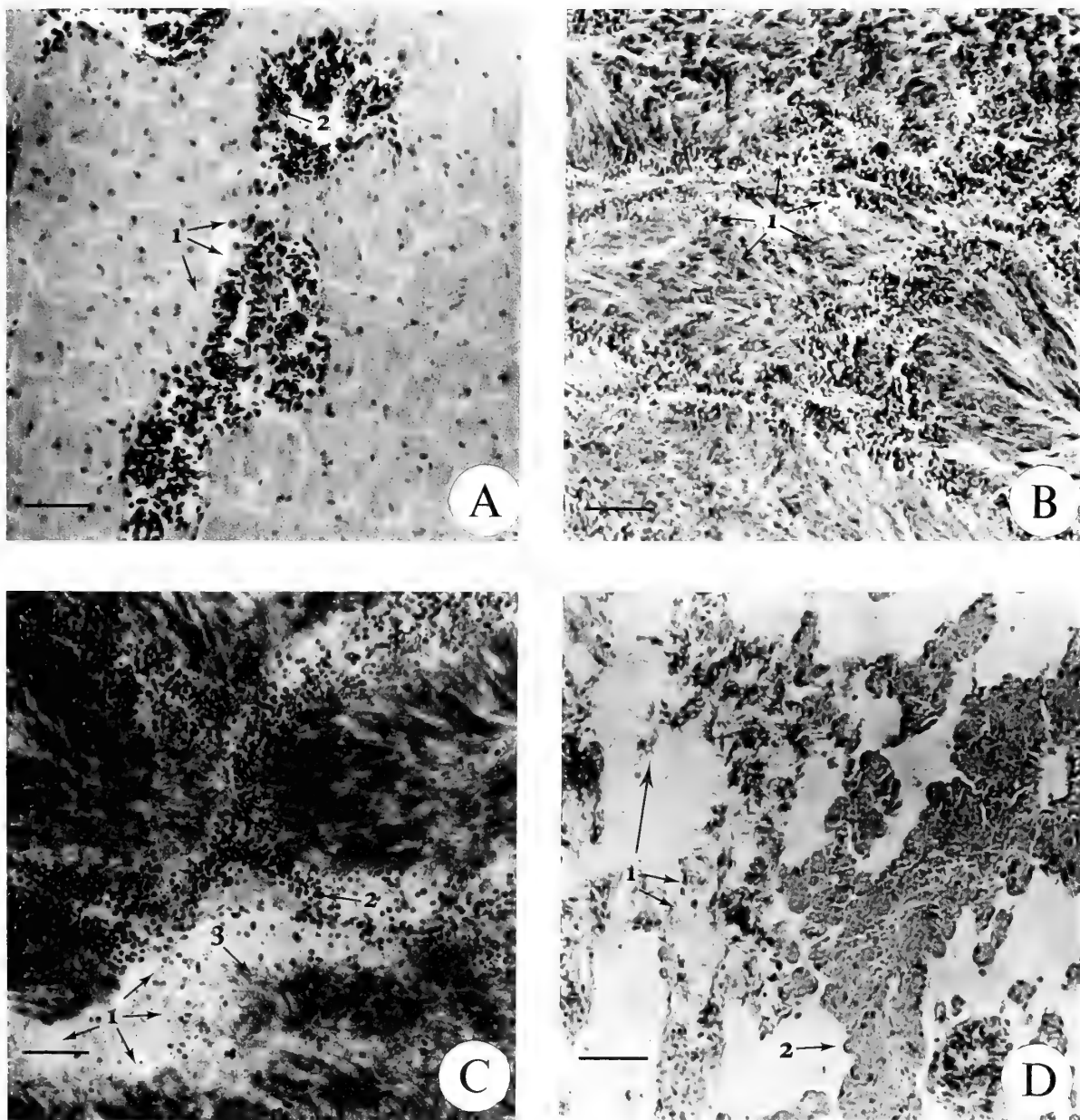


Figure 4

Spermatogenesis in *Glycymeris gigantea*. A. Active in February: (1) Acini with spermatogonia, (2) spermatocytes. B. Ripe in October: (1) Acini full with spermatozoa. C. Spawning in October: (1) Spaces in the lumen of tubule. (2) Spermatocytes. (3) Spermatozoa. D. Spent in December: (1) Residual spermatozoa. (2) Conjunctive Tissue. Scale = 100 μ m.

Ripe. Most oocytes are free within the follicles and are characterized by a polygonal shape. Yolk platelets were observed in the oocyte cytoplasm (Figure 3B). Some oocytes are attached to the wall of follicles by a slender stalk (Figure 2A).

Spawning. Follicles have a moderate amount of ripe oocytes (Figure 3C). The walls of follicles become broken.

There are large spaces inside the follicles and between oocytes. Some follicles are completely devoid of gametes.

Spent. Some residual gametes within follicles and the connective tissue are observed (Figure 3D). Connective tissue begins increasing. The broken follicles are invaded by phagocytes.

Males: Active. The follicles, in different stages of devel-

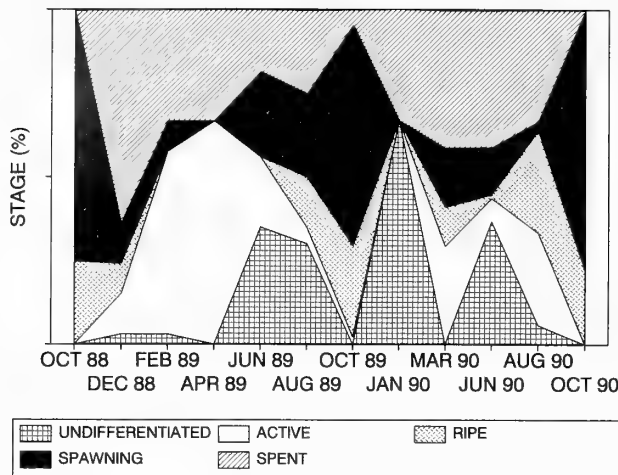


Figure 5

Reproductive cycle of *Glycymeris gigantea*. Frequency of gonadal stages in bimonthly samples between October 1988 and October 1990.

opment, are between the connective tissue. There are varying quantities of germinal cells, spermatocytes, spermatids, and ripe spermatozoa stored until spawning (Figure 2B). The connective tissue between follicles is homogeneous and is formed by cells with fine granulations and pycnotic nuclei (Figure 4A).

Ripe. Almost all the connective tissue has been completely replaced by follicles forming the gonadic tissue, which is occupied by rapid spermatozoa with tails pointing toward the center of the lumen (Figure 4B).

Spawning. In this phase, the walls of follicles become broken and cannot be differentiated. A marked decrease in the number of spermatozoa is observed. There are large spaces inside the follicles (Figure 4C).

Spent. Residual spermatozoa within follicles and the connective tissue are abundant (Figure 4D). The broken follicles are invaded by phagocytes which have irregular shapes, spherical nuclei, and granular cytoplasm.

Reproductive Cycle

The gonad development, observed from October 1988 to October 1990, showed that gametogenesis occurred between February and August (Figure 5). The measurement of oocyte diameters shows gametogenesis having two phases. Between February and April, the oocytes had started to develop close to the acini walls. Starting in August, growth was faster until October, when the oocytes were fully grown (Figure 6). In this month each year, the largest number of ripe and spawning clams were collected. In December and January, the spent and undifferentiated phases were present (Figure 5).

The highest values of Fc were present in October each

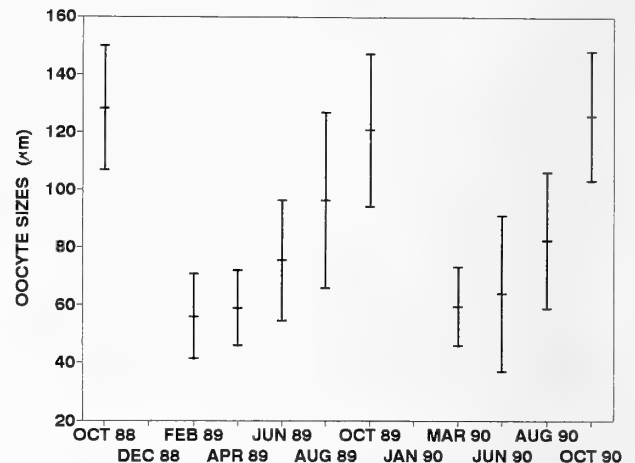


Figure 6

Mean oocyte sizes of *Glycymeris gigantea* between October 1988 and October 1990. Bar = Standard Deviation.

year. The lowest values were obtained in December 1988 and January 1990 (Figure 7).

During the study period, the surface water temperature in Bahía Concepción varied from 16°C to 29°C. The highest values were in summer, August through October, and the lowest from January to March (Figure 8).

DISCUSSION

The characteristics of oogenesis in *Glycymeris gigantea* are similar to those described by Lucas (1965) for *Glycymeris glycymeris* and for other bivalves by Baqueiro & Stuardo (1977); Baqueiro et al. (1982); Manzi et al. (1985); Baqueiro & Masso (1988); Hesselman et al. (1989); and García-Domínguez et al. (1993). During the gametogenic development, five phases were observed: gametogenesis, ripening, gamete expulsion, absorption of residual gametes, and undifferentiated. During the gametogenesis, the follicles increase in size and number, substituting gradually for the abundant connective tissue between follicles. Ripe oocytes have conspicuous yolk platelets and are surrounded by a membrane observed in other species of bivalves, named "chorion" by Sastry (1979) and Sundet & Lee (1984), and "vitelline membrane" by Mackie (1984).

The mean diameter of ripe oocytes of *Glycymeris gigantea* is more than double that of other bivalves found in this area, which have oocyte mean diameters about 70 μm : *Argopecten circularis* (Villalejo-Fuerte & Ochoa-Báez, 1993), *Modiolus capax* (Ochoa-Báez, 1985), and *Megapitaria squalida* (Ochoa-Báez et al., unpublished data). Lucas (1965) found that *Glycymeris glycymeris* has oocytes with oval shapes and 160 to 180 μm diameters.

The spermatozoa are similar to those in *Glycymeris glycymeris* (Lucas, 1965), which have a conspicuous acrosome,

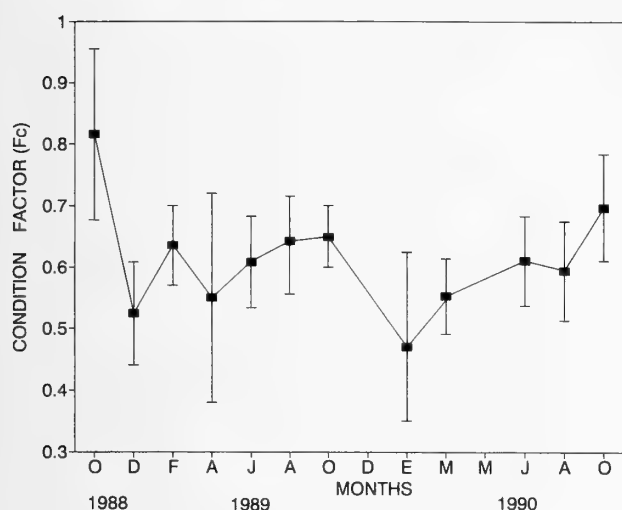


Figure 7

Mean of the condition factor of Fulton (Fc) of *Glycymeris gigantea* between October 1988 and October 1990. Bar = Standard Deviation.

a prominent conic head, and four spherical mitochondria posteriorly. The head and the intermediate piece are 7.5 μ m long.

Temperature is an important environmental factor in the regulation of bivalve reproduction (Sastry, 1979). In *Glycymeris gigantea*, gametogenesis is a slow process and seems to be regulated by temperature. The proliferative phase occurs during the lowest temperatures in winter and spring (17°C to 19°C), and vitellogenesis occurs during the maturation of the oocyte in summer with increasing temperatures (to 30°C). The principal spawning period is in the fall, when temperatures are declining. This same relationship has also been described for other bivalves in Bahía Concepción (Villalejo-Fuerte & Ochoa-Báez, 1993; Ochoa-Báez et al., 1990) and for other species of bivalves from Baja California Sur (Baquero et al., 1981, 1982; Ochoa-Báez, 1985; Baquero & Masso, 1988; García-Domínguez et al., 1993). For populations of bivalves studied in Guerrero, México, it was not possible to find a relationship between the temperature and the reproductive cycle (Baquero & Stuardo, 1977). *Glycymeris gigantea* shows gametogenic activity during the annual cycle with a notable spawning seasonality, the same shown by Muciño & Baquero (in Baquero, 1989) in a study between 1978 and 1979 in Bahía Concepción.

Other species of bivalves abundant in this locality have different reproductive cycles. *Argopecten circularis* has a well-defined spawning period that takes place in the late winter and spring (Villalejo-Fuerte & Ochoa-Báez, 1993), with some reproductive activity throughout the year. *Megapitaria squalida* spawns generally throughout the entire year (Ochoa-Báez et al., unpublished data). These seasonal

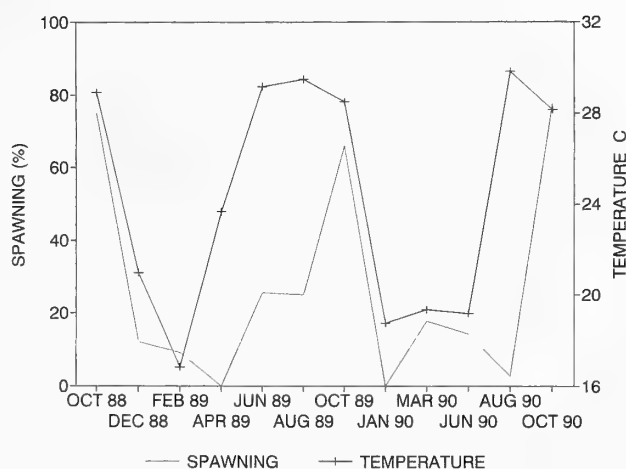


Figure 8

Seasonal variation of mean surface temperature at Bahía Concepción, B.C.S., and frequency of spawning of *Glycymeris gigantea* during the study period.

differences show a considerable diversity in the reproductive patterns of populations of bivalves with temperate-tropical distribution.

The fluctuations of the condition factor are associated with the reproductive or nutritional condition of the mollusks (Searcy-Bernal, 1984). In *Glycymeris gigantea*, the variations of the condition factor seem to be influenced by the gametogenic development. The highest values found in October would be produced by the accumulation of gametes during ripening and spawning, and the lowest values are in December and January during the spent stage. However, the fluctuations of the Fc also may be a consequence of the water contents in the soft body or changes in the mass of nutritive tissue. This suggested that Fc should not be used as an indirect indicator of the spawning season. It is necessary to do a microscopic examination of the gonads.

ACKNOWLEDGMENTS

The authors are grateful to Dirección de Estudios de Postgrado e Investigación del Instituto Politécnico Nacional México, from which the project "Estudio de poblaciones de moluscos de importancia económica," number 880604, provided the funds to make this research possible. We thank Arturo Tripp Quezada M. SC. for collecting some of the specimens, and Dr. Ellis Glazier for his help in editing the English manuscript.

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Polygyrid Land Snails, *Vespericola*
(Gastropoda: Pulmonata), 2. Taxonomic Status of
Vespericola megasoma (Pilsbry) and
V. karokorum Talmadge

by

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Abstract. A type locality is designated for *Vespericola megasoma* (Pilsbry, 1928) and the species redescribed. *Vespericola megasoma* has a diagnostic spoon-shaped verge at the apex of the penis. *Vespericola eritrichius* (Berry, 1939), formerly synonymized with *V. megasoma*, is shown to be a valid species. The anatomy of *Vespericola karokorum* Talmadge, 1962, is described. *Vespericola karokorum* is localized in a few stream drainages in the Klamath Mountains. It has a diagnostic acicular verge nearly as long as the penis. Populations of *Vespericola* from several stream drainages adjacent to the range of *V. karokorum*, formerly referred to *V. megasoma*, are described as a new species, *Vespericola klamathicus*.

INTRODUCTION

This is the second (with Roth & Miller, 1993) in a series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. The greatest species diversity occurs in northwestern California and southwestern Oregon, where seven nominal taxa have been recognized.

Dissections of the reproductive system, which in *Vespericola* is often more strikingly differentiated than the shell, show that the concept of *Vespericola megasoma* (Pilsbry, 1928) employed in the last monograph of the genus (Pilsbry, 1940) included several distinct species. To clarify the definition of *V. megasoma*, which was described on shell characters alone and with a generalized type locality, we designate a type locality and describe the reproductive systems of topotypic specimens. *Vespericola eritrichius* (Berry, 1939), which Pilsbry (1940) regarded as synonymous with *V. megasoma*, is here regarded as a valid species, based on reproductive system characters.

Land snail taxonomists generally have accepted *Vespericola karokorum* Talmadge, 1962, as a valid species, but a report to the U.S. Forest Service (Hunt & DeMartini, 1979) called into question its distinctness from *V. megasoma*. We describe the reproductive system of *V. karokorum* and compare the species to *V. megasoma*. A species from

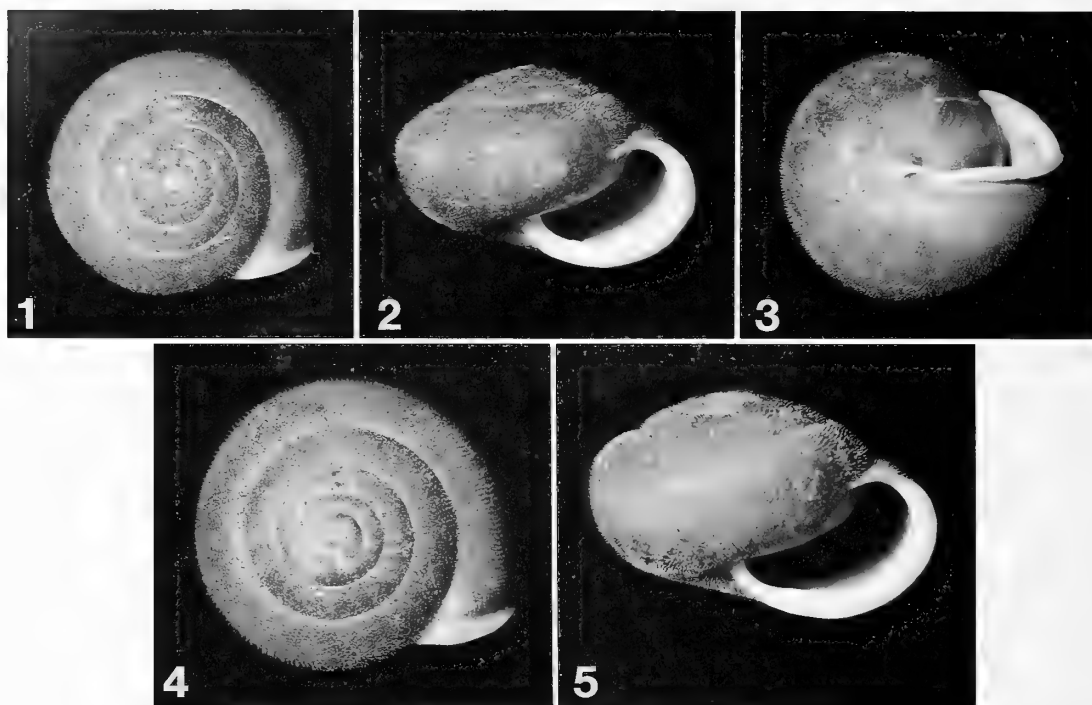
drainages adjacent to the range of *V. karokorum*, incorrectly identified by Hunt & DeMartini (1979) as *V. megasoma*, is described herein as a new species, *Vespericola klamathicus*.

MATERIAL AND METHODS

The authors collected material of the taxa discussed in this paper from 1968 to 1992; additional specimens of many were located in museum collections. Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of Pilsbry (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 30× magnification under a dissecting microscope with an ocular reticle. Three counts were taken per specimen and the mean (to the nearest integer) recorded.

Specimens for dissection and whole mounts of genitalia were prepared by the methods described by Roth & Miller (1993).

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; BR, senior author's collection, San Francisco, California; CAS, California Academy of Sciences; FMNH, Field Museum of Natural



Figures 1-5

Vespericola megasoma (Pilsbry). Figures 1-3. Topotype, shell, BR 1743, CALIFORNIA: Humboldt County: along right bank of Prairie Creek near south end of Prairie Creek Redwoods State Park. W. B. Miller, B. Roth coll., 11 February 1991; top, side, and basal views. Diameter 12.7 mm. Figures 4, 5. Shell, BR 1728, CALIFORNIA: Marin County: Inverness. B. Roth, W. B. Miller coll., 29 April 1990; top and side views. Diameter 15.1 mm.

History, Chicago; LACM, Los Angeles County Museum of Natural History; MCZ, Museum of Comparative Zoology, Harvard University; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, United States National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

Polygyridae Pilsbry, 1895

Vespericola Pilsbry, 1939

Vespericola Pilsbry, 1939:xvii. Pilsbry, 1940:892-894. Zilch, 1960:586. Roth & Miller, 1993:135.

Type species: *Polygyra columbiana pilosa* Henderson, 1928 [= *Vespericola pilosus* (Henderson)], by original designation.

Vespericola megasoma (Pilsbry, 1928)

(Figures 1-8)

(?) *Polygyra germana* variety *megasoma* Dall, 1905:26 [*nomen nudum*].

Polygyra columbiana megasoma Dall, Pilsbry, 1928:182-183, 185, figs. 8, 8a, 9.

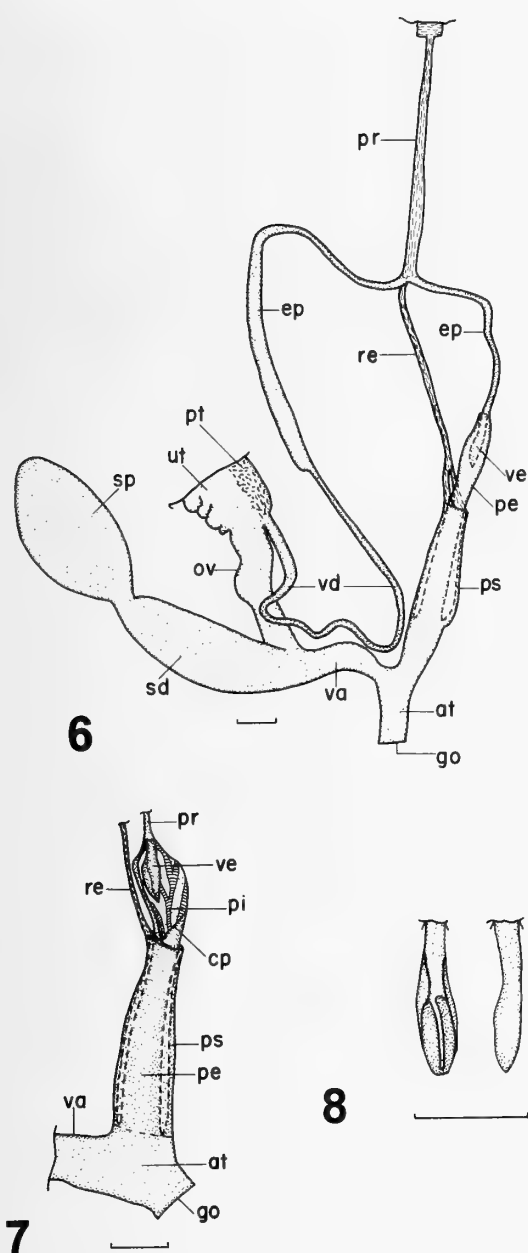
Vespericola megasoma ('Dall,' Pilsbry), Pilsbry, 1940:894,

904-909 (in part), figs. 512B; 513:8, 8a, 9; 519. Ingram, 1946:93. Ingram & Lotz 1950:26-27, pl. 5, figs. 9, 10.

Polygyra megasoma 'Dall,' Pilsbry, Baker, 1962:13.

Diagnosis: A small to medium-sized *Vespericola* with depressed-globose, almost imperforate shell of 5.5-6.0 whorls; periostracal setae 25-70/mm². Penis short, about half enclosed in sheath; with moderately long, spoon-shaped verge; spermathecal complex massive, larger than penial complex.

Description of shell: Shell depressed-globose, with 5.5-6.0 whorls. Spire moderately elevated, straight-sided or slightly convex; suture moderately impressed; whorls slightly shouldered. Periphery broadly rounded, sometimes slightly compressed toward shell axis. Embryonic whorls with smooth initial tip, thereafter rather coarsely papillose, papillae tending to fuse into collabral rugae. Post-embryonic sculpture of low, retractive growth rugae, strongest below suture. Periostracum bearing dense pile of short, closely spaced, erect, acute setae in steeply descending rows. Setae variable in density, 24-70/mm². (Paratype with 33-34 setae/mm²; holotype with glue at the usual spot where we measure setae, but right behind it, 30 ± 3 setae/mm².) Surface between setae with very fine, predominantly axial, wrinkling, sometimes elaborated into minute scales. Base



Figures 6–8

Vespericola megasoma (Pilsbry). Drawings made from projection of stained whole mounts. Scale line = 1 mm. Figure 6. Anterior portion of reproductive system of topotype, SBMNH 78000, CALIFORNIA: Humboldt County: along right bank of Prairie Creek near south end of Prairie Creek Redwoods State Park. W. B. Miller, B. Roth coll., 11 February 1991. Figure 7. Anterior portion of reproductive system of specimen SBMNH 77924, with apex of penis opened to show verge and papillose pilasters; CALIFORNIA: Humboldt County: confluence of Jordan Creek and Eel River. W. B. Miller coll., 11 April 1990. Figure 8. Ventral and lateral views of verge of specimen SBMNH 77935, OREGON: Curry County: Ophir, in willows behind beach. W. B. Miller coll., 24 September 1990. Abbreviations used in anatomical drawings: at, atrium; cp, cut edge of penis; ep, epiphallus;

tumid, solid-looking, radially wrinkled, densely papillose where setae worn off. Umbilicus a minute, oblique perforation. Body whorl deep, deflected downward just behind lip. Aperture broadly auriculate; plane of aperture at angle of 28° to shell axis. Lip turned outward and reflected, strongly thickened. Parietal callus extending well to left of columella in basal view. Low parietal lamella often present. Inner part of basal lip straight, narrowed. Inner lip dilated backward so as to enclose umbilicus from left side. Periostracum brown (faded to tan in holotype and paratype); lip white; yellowish-cream specimens occasionally found.

Dimensions of holotype: Diameter (exclusive of expanded lip) 12.5 mm, height 8.8 mm, whorls 5.75.

Measurements and counts of material at hand: Range of adult shell diameter 11.3–15.1 mm (mean of 45 specimens including holotype, 12.85 mm); height, 6.9–10.3 mm (\bar{x} = 8.93 mm); height/diameter ratio, 0.61–0.82 (\bar{x} = 0.694); number of whorls, 5.2–6.1 (\bar{x} = 5.61).

Description of soft anatomy: Eleven topotypes from Prairie Creek Redwoods State Park were dissected. A total of 111 specimens from various other localities was dissected.

Living animal light tan to pinkish buff along foot, darker and grayish brown on body-stalk. Mantle over the lung 10–30% maculated with black.

Atrium (Figure 6) of moderate length for the genus. Penis elongate-conical, with anterior, basal half enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in figured topotype about 3.0 mm long; protruding part about 2.6 mm long. In remaining topotypes, sheathed part 2.4–3.3 mm (mean 2.8 mm); protruding part 2.4–3.6 mm (mean 3.0 mm). Ratio of protruding length to sheathed length 1.18–0.43 (mean about 1.0). Peduncular section of about 1.5 mm present between base of sheath and junction with atrium. Apex of penis containing moderately long, spoon-shaped verge, 1.2–1.4 mm long, 0.2 mm wide at base (Figures 7–8). Seminal duct opening into penial chamber at tip of verge through open, terminal groove with thickened edges. Inner wall of penis with papillose, anastomosing, more or less oblique pilasters.

Spermathecal duct massive, appressed to the free oviduct (which is smaller in diameter and branches from it), elongate-ovate, about 4.5 mm long, about 1.0 mm in diameter at junction with oviduct, gradually enlarging to maximum of 1.7 mm before tapering to 0.5 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature

←

go, genital orifice; ov, oviduct; pe, penis; pi, pilaster; pr, penial retractor; ps, penial sheath; pt, prostate; re, retentor; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vd, vas deferens; ve, verge.

specimens, narrowly cylindrical in less mature individuals, about 4.5 mm long, with rounded tip.

Type material: *Holotype*: ANSP 11140a (shell), CALIFORNIA: Humboldt County. H. Hemphill coll. Type locality here restricted to: CALIFORNIA: Humboldt County: right (east) bank of Prairie Creek, near south end of Prairie Creek Redwoods State Park.

Paratype: ANSP 11140 (shell), with same locality data as holotype.

Referred material: OREGON: Curry County: Humbug Mountain (SBMNH); Ophir (SBMNH 77935). CALIFORNIA: Humboldt County: Prairie Creek Redwoods State Park (BR 1743, CAS 047737, SBMNH 78000); Trinidad (SBMNH); Table Bluff (BR 1744, SBMNH); ravine between E bank of Eel River and Shively Road, 10.6 km E of junction with U.S. Highway 101 (BR 1745, SBMNH); Jordan Creek at confluence with Eel River (SBMNH 77924). Mendocino County: Chadbourne Gulch (SBMNH); mouth of Tenmile River (CAS, SBMNH). Sonoma County: Green Valley (SBMNH); Hampton Road, N of Occidental (BR 1330); Wright Beach (BR 1669, SBMNH); Portuguese Beach (BR 413, SBMNH); 3.2 km N of Freestone (BR); Salmon Creek at Freestone (BR 1862). Marin County: Inverness (BR 1728, CAS 052393, SBMNH; Pilsbry, 1940).

Remarks: Following the monograph of Pilsbry (1940), the name *Vespericola megasoma* generally has been applied to specimens in which the inner part of the basal lip, in umbilical view, is straight or very weakly deflected forward, and the inner lip is fan-shaped and dilated such that its free edge encroaches on the umbilicus from the left side. The holotype is a shell of this type. Material with this character, however, includes several genital types that undoubtedly represent separate species, raising the question of the identity of "true" *V. megasoma*.

The first use of the epithet "*megasoma*" was Dall's (1905) *Polygyra germana* variety *megasoma*, a *nomen nudum*. Pilsbry (1928) validly described the species, attributing the name to Dall as a courtesy but not using Dall specimens or manuscript. No manuscript type material of *Polygyra germana* variety *megasoma* Dall is known to exist (Pilsbry, 1928; Boss, Rosewater, & Ruhoff, 1968). Pilsbry (1928) based his description on a shell received from Henry Hemphill. The original label states, in Hemphill's writing: *Helix columbiana* var. / Humboldt Co. Cal. Pilsbry (1928, 1940) and Baker (1962) referred to the type specimen as a neotype, but because the name was validly proposed first by Pilsbry (1928), it is a holotype.

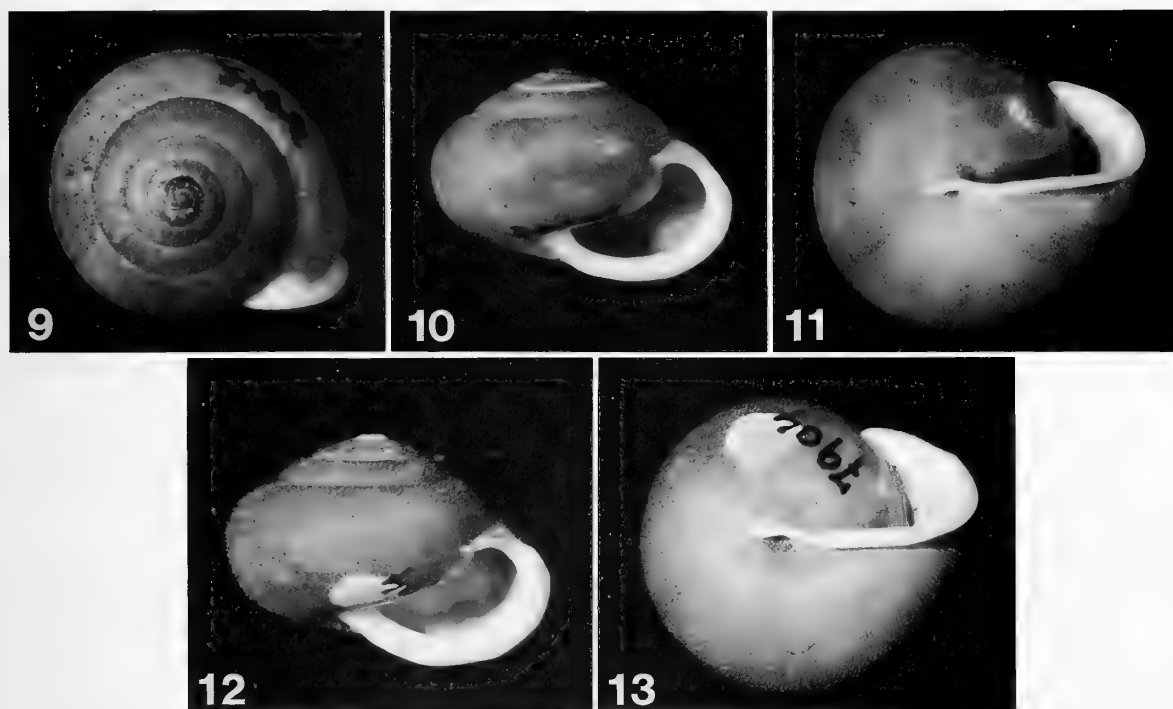
Shells with shape, dimensions, whorl count, and setation like the holotype and paratype occur in the population along the east bank of Prairie Creek, near the south end of Prairie Creek Redwoods State Park, Humboldt County, California. We designate this locality as the type locality of *Vespericola megasoma*. No other historical records exist to indicate where Hemphill might have collected the holotype; indeed, he sometimes lumped under a single locality

specimens from numerous stations (Coan & Roth, 1987). However, the designated type locality is and has long been accessible from the main north-south road (now U.S. Highway 101) through northwestern California and is at least as plausible as any other potential type locality.

The reproductive system of specimens from the type locality is as described above, with moderately large, spoon-shaped verge in a rather small, slender, cylindrical penis; sheathed and protruding parts of the penis about equal in length; and a massive spermathecal complex larger than the penial complex. These characters distinguish *V. megasoma* from all other species. *Vespericola eritrichius*, which Pilsbry (1940) synonymized with *V. megasoma*, differs in having a short, conical verge in a longer penis, and a longer vagina with a fleshy thickening just below the origin of the spermathecal duct. *Vespericola klamathicus*, sp. nov., described below, has a short, conical verge with a cleft tip, and a longer penis. Several other species with distinctive genital types occur in northern California and will be described in a later paper.

Vespericola megasoma is the most widespread of the species with "*V. megasoma*-type" shells. Associating the name *V. megasoma* with the presence of a spoon-shaped verge (as we have done by designating the type locality above) preserves the accepted meaning of the name to the greatest extent possible. It means that most literature references and museum lot identifications of *V. megasoma* probably remain correct. However, especially with specimens from new localities, it is always desirable to establish a sample's identity by dissection.

Identifications of specimens from the localities listed above have been confirmed by dissection. In addition, we have noted shells of the *V. megasoma* type in museum and private collections from the following localities. Some, perhaps most, may represent *V. megasoma*, but pending examination of the anatomy of specimens from these localities, we regard this material as indeterminate: OREGON: Douglas County (CAS 052416; Pilsbry, 1940); Elkton (CAS 047735). Josephine County: 5.6 km SW of Wilderville (BR 389). Curry County: Pistol Creek Camp (SBMNH). CALIFORNIA: Del Norte County: near Fort Dick (CAS 052391); 5 km N of Crescent City (CAS 047743; Pilsbry, 1940); Smith River near Hiouchi Bridge (BR 579, SBMNH); 5 km below Hiouchi Bridge (SBMNH); woods near Crescent City (Pilsbry, 1940); Crescent City (CAS 047736); Enderts Beach (BR 578; CAS 047733); E side of Howland Hill (Pilsbry, 1940); Del Norte Coast Redwoods State Park (BR 577); 3.2 km N of Requa (CAS 052380); Terwah (CAS 052266; CAS 052403); across Klamath River from Requa (Pilsbry, 1940); Chaffey Ranch, 11 km above mouth of Klamath River (SBMNH). Humboldt County: 5 km N of Orick (CAS 052271); mouth of Redwood Creek (BR 1000); Orick (CAS 047740, CAS 047744, CAS 047748, CAS 049817); Moonstone Beach (BR); Clam Beach (BR 352; Pilsbry, 1940); McKinleyville (BR 351); between McKinleyville and Mad River (CAS 052414); near Eureka (CAS 046504, CAS 047730, CAS



Figures 9-13

Vespericola eritrichius (Berry). Figures 9, 11. Paratype, shell, SBMNH 34245, top and basal views. Diameter 15.7 mm. Figure 10. Holotype, shell, SBMNH 34244. Diameter 14.4 mm. Figures 12, 13. Shell, SBMNH 77904, CALIFORNIA: Humboldt County: ravine between E bank of Eel River and Shively Road 10.6 km E of U.S. Highway 101. W. B. Miller coll., 12 April 1990; side and basal views. Diameter 14.0 mm.

047731, CAS 052415, CAS 052418; Pilsbry, 1940); Grizzly Creek (SBMNH); near Ferndale (SBMNH); sea cliff S of Centerville Beach (BR 339); Capetown (BR 328, SBMNH); Little Burr Creek, 8 km SE of Bridgeville (SBMNH); Pepperwood (SBMNH); Bridge Creek (SBMNH); Dyerville (BR 273); Miranda (BR 1186); Weott (CAS 052423) and 13 km E (BR 245, SBMNH); Fort Seward (BR 278); S Fork of Eel River near Canoe Creek (SBMNH); near Richardson Grove (BR 1746). Mendocino County: Red Mountain Creek (SBMNH); DeVey Redwood Park, S Fork of Eel River (BR); 4.6 km S of Rockport (SBMNH); N Fork of Juan Creek (CAS 052283, SBMNH); 18 km N of Fort Bragg (CAS 047754, CAS 052408); Van Damme State Park (CAS 052277, CAS 052410); 1.6 km S of Little River (CAS 052412); Navarro (BR 285, CAS 052335); Irish Gulch (BR 1673, SBMNH); Anchor Bay (SBMNH); 6.4 km E of Anchor Bay (CAS 052407). Sonoma County: 7 km S of Stewarts Point (SBMNH); Rio Nido (CAS 052357, CAS 052369); Sonoma (CAS 047811); mouth of Russian River (BR 1680); Smith Creek (CAS 047792, CAS 047793); Forestville (BR 573).

Vespericola megasoma is found in a wide variety of habitats: among moist ferns, grasses, *Rubus* vines, moss, horsetails (*Equisetum* spp.), salal (*Gaultheria shallon*), and other

coastal brushfield vegetation; in redwood forest. At Table Bluff Light, Shively Road, and Chadbourne Gulch it is sympatric with *Vespericola eritrichius*.

Vespericola eritrichius (Berry, 1939)

(Figures 9-16)

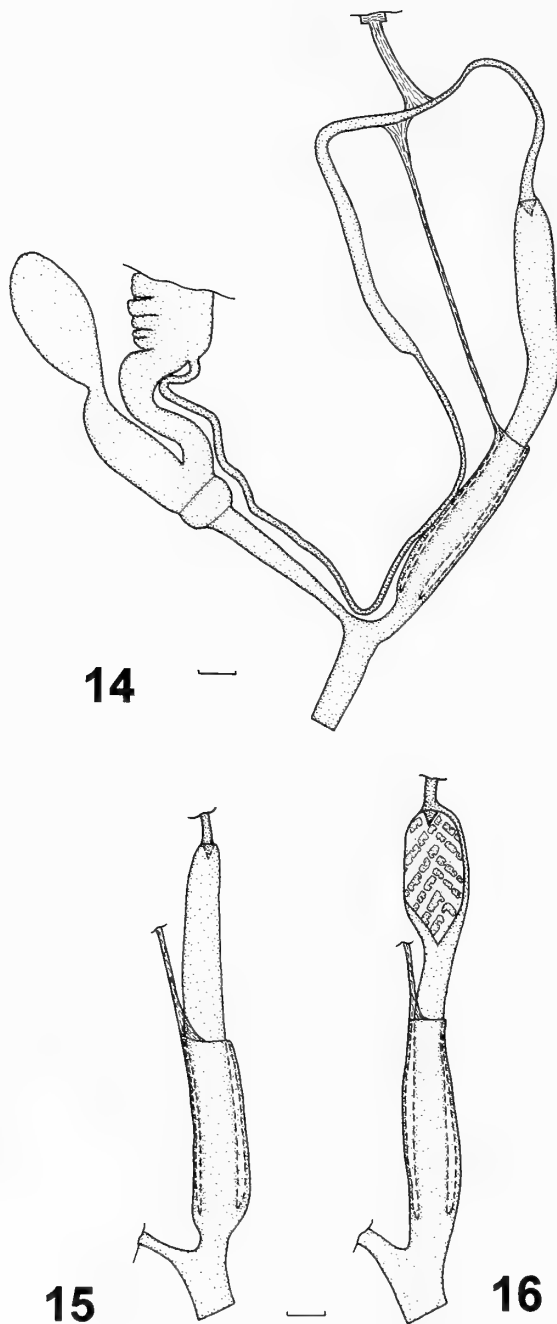
Mesodon (*megasoma*, subsp.?) *eritrichius* Berry, 1939:56, figs. 1B, 1C.

Vespericola megasoma ('Dall' Pilsbry), Pilsbry, 1940:904, 907-909 (in part), figs. 520B, 520C.

V[espericola]. eritrichius (Berry), Talmadge, 1962:29.

Diagnosis: A medium-sized *Vespericola* with depressed-globose, almost imperforate shell of 5.3-5.9 whorls; periostracal setae 12-34/mm². Penis long, slender, approximately half enclosed in sheath; with small, short, conical, pointed verge, 0.4-0.5 mm long; spermathecal duct thick, ovate or cylindrical, abruptly tapering to constriction at spermatheca.

Description of shell: Shell of medium size for the genus, compact, depressed-globose, almost imperforate, of 5.3-5.9 whorls; base inflated, solid-looking. Spire broadly conic, moderately elevated, its sides weakly convex; whorls somewhat flattened, suture shallowly impressed. Embry-



Figures 14-16

Vespericola eritrichius (Berry). Drawings made from projection of stained whole mounts. Scale line = 1 mm. Figure 14. Anterior portion of reproductive system of specimen SBMNH 77904, CALIFORNIA: Humboldt County: ravine between E bank of Eel River and Shively Road 10.6 km E of U.S. Highway 101. W. B. Miller coll., 12 April 1990. Figure 15. Penis of topotype, SBMNH 77815, CALIFORNIA: Humboldt County: base of Table Bluff. W. B. Miller coll., 9 July 1989. Figure 16. Penis of specimen SBMNH 78003, with apical portion cut open to show verge and papillose pilasters; locality same as in Figure 14 above, W. B. Miller, B. Roth coll., 11 February 1991.

onic whorls 1.4–1.6, projecting, sculptured with crowded, round or radially elongate papillae that tend to align in radiating rows separated by shallow grooves. Early neanic whorls with fine, slightly retractive growth rugae and rather sparse, erect, acicular setae in protractive, descending rows. Setae not obviously forked at base, often with small, finlike basal extension abaperturally. Periostracum between setae radially wrinkled and densely granulose with a collabral trend, some granules elaborated into minute scales. Setae closer together and shorter on subsequent whorls; 12–34 setae/mm² on shoulder of body whorl behind lip. Body whorl deep; periphery inflated, broadest just above middle of whorl. Base densely and regularly setose. Last whorl not markedly descending, sharply constricted behind lip. Aperture auriculate, peristome weakly concave in profile, oblique, at angle of about 35° to vertical; lip expanded and reflected, most strongly at base, well thickened with callus. Umbilical crevice extremely narrow, oblique. Inner part of basal lip straight or weakly kinked forward, sometimes bearing small callus nodule; inner lip dilated so that it encroaches on, and nearly covers, umbilicus from left side. Parietal callus granulose, free edge strongly convex, swinging well to left of umbilicus, with shallow sinus below upper limb of peristome. Minute, white or translucent parietal lamella usually present on inner part of parietal callus. Shell light reddish brown or yellowish brown, zone of internal callus thickening behind peristome lighter; peristome cream-colored.

Dimensions of holotype: Diameter 14.4 mm, height 10.2 mm, whorls 5.8.

Measurements and counts of material at hand: Range of adult shell diameter 11.0–14.4 mm (mean of 22 specimens including holotype, 13.09 mm); height, 8.2–10.9 mm (\bar{x} = 9.55 mm); height/diameter ratio, 0.68–0.78 (\bar{x} = 0.730); number of whorls, 5.3–5.9 (\bar{x} = 5.66).

Description of soft anatomy: Only one topotype was found; its dissection revealed a distinctive penial complex (Figure 15), but the spermathecal complex was immature. Mature specimens from another locality are illustrated in Figures 14 and 16. Ten other specimens from different localities were dissected to determine the range of variation in diagnostic structures.

Living animal tan along foot with occasional pinkish cast along edge, darker and grayer on body stalk. Mantle over lung clear buff, 20–40% maculated with black.

Atrium (Figure 14) moderate to long for the genus. Penis long, cylindrical, moderately slender, gradually tapering at apex; with anterior half enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Thin retentor muscle extending from penial retractor at attachment on epiphallus to summit of penial sheath, from which other fibers connect with parts of epiphallus and vas deferens. Sheathed part of penis in topotype about 4.5 mm long; protruding part about 5.2 mm long. In other specimens, sheathed part 4.0–5.6 mm (mean 5.0 mm);



Figures 17–19

Vespericola karokorum Talmadge. Shell, SBMNH 78124, CALIFORNIA: Humboldt County: Wilson Creek, ca. 2.5 mi [4.0 km] NE of Orleans, upstream (west) of Ishi Pishi Road, W. B. Miller, B. Roth coll., 9 April 1992; top, side, and basal views. Diameter 15.0 mm.

protruding part 4.0–6.6 mm (mean 5.5 mm). Ratio of protruding length to sheathed length 0.87–1.47 (mean about 1.1). Slender peduncular section of about 1.0 mm present between base of sheath and junction with atrium. Apex of penis containing short, conical, pointed verge, 0.4–0.5 mm long, 0.4 mm wide at base. Seminal duct opening into penial chamber at tip of verge. Inner wall of penis with discontinuous, diverging, papillose pilasters (Figure 16).

Spermathecal duct in fully mature specimens massive, tightly appressed to free oviduct (which is smaller in diameter and branches from it), ovate or cylindrical, about 4.0 mm long, about 1.5 mm in diameter at junction with oviduct, tapering somewhat abruptly to 0.5 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens and narrowly cylindrical in less mature individuals, averaging about 3.8 mm in length, with rounded tip.

Vagina notably long and slender for the genus. Fleishy thickening present around vagina just below junction of oviduct and spermathecal duct in fully mature specimens, partially formed or absent in immature specimens.

Type material: *Holotype*: SBMNH 34244 (shell). CALIFORNIA: Humboldt County: foot of bluff on ocean side of peninsula at Table Bluff Light; among moist ferns, poison oak, wild blackberries, *Equisetum*, etc. L. Shapovalov, E. H. Vestal coll.

Paratypes: CAS 064419 (shell), CAS 065908 (shell), SBMNH 34245 (11 shells), from same locality as holotype.

Referred material: CALIFORNIA: Humboldt County: base of Table Bluff, SW end of Humboldt Bay (BR, SBMNH 77815); S bank of Eel River at highway bridge at Fernbridge (SBMNH); ravine between E bank of Eel River and Shively Road, 10.6 km E of junction with U.S. Highway 101 (BR, SBMNH 77904, SBMNH 78003). Mendocino County: Chadbourne Gulch (SBMNH); Frank and Bess Smithe Redwoods State Park (SBMNH).

Remarks: Two species of *Vespericola* occur sympatrically at Table Bluff, the type locality of *V. eritrichius*: *Vespericola megasoma* with its diagnostic spoon-shaped verge, and a second species in which the penis is longer and the verge is small and conical, with the seminal duct opening at the tip. Our dissected topotype (Figure 15) had 22 setae/mm² on the body whorl and penultimate whorl; confirmed *V. megasoma* from the same locality had 25, 36, and 40 setae/mm². Among all dissected specimens with small conical verge and anatomy as described above, setae ranged from 12 to 34 (\bar{x} = 20.1; n = 12).

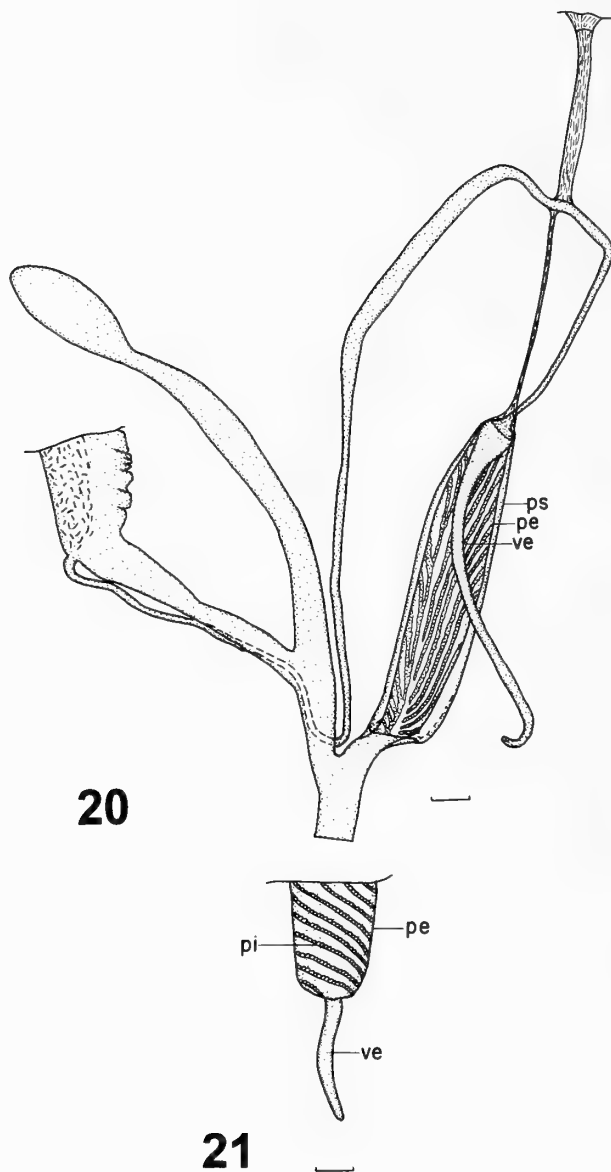
Vespericola eritrichius was described solely from shells. The holotype has 19 setae/mm². We cannot rule out the possibility that it may have had a spoon-shaped verge, but on the basis of the relatively low count of setae, we interpret it as belonging to the species with a small conical verge. The paratypes have 28–34 setae/mm²; some or all are probably *V. megasoma*. (There is a double irony in the fact that, although Berry emphasized dense setation in the description and name of *V. eritrichius*, the holotype is the specimen from the type lot with the sparsest setae—and also the one that is most probably not *V. megasoma*.)

Vespericola eritrichius is distinguished anatomically from other species by its very short conical verge in a long, narrow, cylindrical penis, of which the protruding portion is about equal to or longer than the sheathed portion, in combination with a massive spermathecal duct and a fleshy ring at the apical end of a long, slender vagina. There appear to be no shell characters that will always separate *V. eritrichius* from *V. megasoma*.

Talmadge (1962) treated *V. eritrichius* as a distinct species but did not discuss his reasons for doing so.

Vespericola eritrichius is found along streams, in willows and ferns; in coastal brush; and under logs and in leaf litter in mixed evergreen forest.

For purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988) and



Figures 20–21

Vespericola karokorum (Talmadge). Drawings made from projections of stained whole mounts. Scale line = 1 mm. Figure 20. Anterior part of reproductive system of topotype, SBMNH 78119, CALIFORNIA: Humboldt County: Sawmill Gulch between Ishi Pishi Road and Klamath River, W. B. Miller, B. Roth coll., 8 April 1992; penis cut open to show pilasters and verge. Figure 21. Everted penis and protruding verge, topotype, BR 1438, CALIFORNIA: Humboldt County: Sawmill Gulch between Ishi Pishi Road and Klamath River, B. Roth coll., May 1981.

other administrative uses, we proposed the name “velvet hesperian.”

Vespericola karokorum Talmadge, 1962

(Figures 17–21)

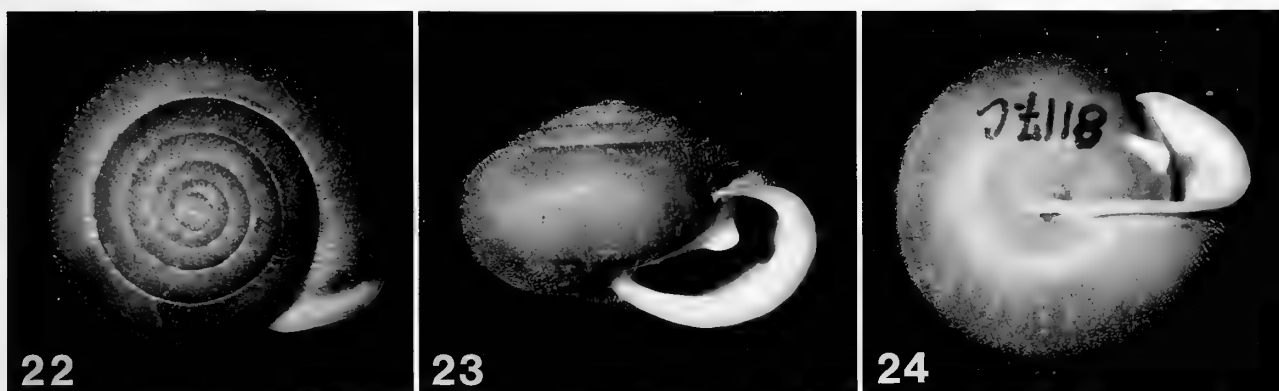
Vespericola karokorum Talmadge, 1962:28–29, pl. 5, figs. 1–3. Sphon, 1971:26.

Diagnosis: A medium-sized to large *Vespericola* with depressed-conic, almost imperforate shell of 5.5–6.2 whorls; periostracal setae approximately 2/mm². Penis approximately 70% enclosed by sheath; with 10 mm long, acicular verge which extends below sheathed part of penis into peduncular section.

Description of shell: Shell medium-sized to large for the genus, depressed-conic, of 5.5–6.2 whorls; base compressed; umbilicus minute, usually not visible in direct basal view. Spire low, very broadly conic, its sides straight or weakly convex; whorls well rounded, suture moderately to strongly impressed. Embryonic whorls 1.5, first 0.25 whorl smooth, thereafter sculptured with riblets radiating from suture, almost entirely broken into rows of radially elongate papillae that tend to fade out at or just above periphery. Early neanic whorls with fine growth rugae and sparse, translucent, erect, gently curving, acicular setae in very shallowly descending rows (also aligning in nearly collabral series). Setae minute at first but rapidly increasing in size, to 0.4 mm long on third whorl, 1.0 mm on fourth whorl; longest setae, on periphery of body whorl, 1.1–1.3 mm long; spacing of setae generally about 2/mm². Zone of small (0.2 mm or less) setae usually present just below suture. Periostracum between setae densely granulose. Periphery rounded to subangulate, broadest above middle of whorl, somewhat sloping toward base. Base setose like rest of body whorl, with zone of smaller setae around umbilical region. Last whorl not markedly descending; last 0.2 turn sometimes rising slightly on penultimate whorl; body whorl sharply constricted behind lip. Aperture broadly auriculate, peristome concave in profile, oblique, at angle of about 45° to vertical; lip strongly expanded, reflected at base, thickened submarginally. Umbilical crevice extremely narrow, oblique. Basal lip straight to gently arched; inner part narrowed, often with a small callus nodule. Inner lip excavated, deeply entering at columella, dilated so that it encroaches on, and nearly covers, umbilicus from front. Parietal callus smooth, shining, with fine granulation, free edge convex, swinging to left of umbilicus, with small sinus below upper limb of peristome. Prominent, short, elevated, white parietal lamella present. Shell light golden brown; peristome light orange to pinkish tan.

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.2 mm, height 8.9 mm, whorls 5.9.

Measurements and counts of material at hand: Range of adult shell diameter 12.5–16.2 mm (mean of 36 specimens



Figures 22–24

Vespericola klamathicus Roth & Miller, sp. nov. Holotype, shell, SBMNH 142588, CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992; top, side, and basal views. Diameter 16.0 mm.

including holotype, 14.57 mm); height, 7.5–9.5 mm (\bar{x} = 8.73 mm); height/diameter ratio, 0.55–0.64 (\bar{x} = 0.600); number of whorls, 5.5–6.2 (\bar{x} = 5.89).

Description of soft anatomy: Three topotypes and five specimens from a nearby locality (Wilson Creek) were dissected.

Living animal light tan to pinkish buff along foot, darker and grayer on body-stalk. Mantle over the lung clear buff, 25–40% maculated with black.

Atrium (Figure 20) of moderate length for the genus. Penis long, slender, cylindrical, with about 70% of its length enclosed in thin sheath adnate to base. Penial retractor muscle inserted on epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in figured topotype about 6.0 mm long; protruding part about 2.8 mm long. In other specimens, sheathed part 4.5–5.8 mm (mean 4.9 mm); protruding part 0–3.4 mm (mean 1.1 mm). Ratio of protruding length to sheathed length averaging about 0.3. Slender peduncular section of about 1.5 mm present between base of sheath and junction with atrium. Apex of penis containing very long, slender, acicular verge 10.0 mm long and 0.9 mm wide at its base, which extends below sheathed part of penis and recurves into peduncular section. Seminal duct opening in minute terminal cleft of verge. Inner wall of penis with oblique papillose pilasters, some of which fuse at their lower ends (Figure 20).

Spermathecal duct long, slender, cylindrical, appressed to free oviduct (which is smaller in diameter and branches from it), about 9.3 mm long, about 1.0 mm in diameter at its junction with the oviduct, tapering gradually to 0.4 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical

in less mature individuals, about 4.4 mm long, with rounded tip.

Type material: *Holotype*: CAS 064088 (shell), CALIFORNIA: Humboldt County: Sawmill Gulch, on Ishi Pishi Road, 2.0 mi [3.2 km] east [NE] of Orleans Ranger Station. R. R. Talmadge coll., July 1961.

Paratypes: BR 1166, CAS 064089 (shells), from same locality as holotype. Additional paratypes stated to be deposited in ANSP, FMNH, LACM, MCZ, SDNHM, USNM, and various private collections (Talmadge, 1962).

Referred material: CALIFORNIA: Humboldt County: Wilson Creek, ca. 2.5 mi [4.0 km] NE of Orleans, upstream (west) of Ishi Pishi Road (BR 1762, SBMNH 78124); Sawmill Gulch, east and west of Ishi Pishi Road (BR 107, BR 1167, BR 1438, BR 1758, SBMNH 78119); N side of Sawmill Gulch (CAS 053475).

Remarks: *Vespericola karokorum* is distinguished anatomically from other species by its extremely long verge and long spermathecal duct. In no other known species of *Vespericola* does the verge come close to equalling the length of the penis. In concluding that *V. karokorum* was a “microgeographic race” of *V. megasoma*, Hunt & DeMartini (1979) evidently did not examine the verges. *Vespericola karokorum* also differs from the other species described herein in that the penial sheath covers well over half of the penis (occasionally reaching the apex of the penis), and the spermathecal duct is slender and cylindrical, not swollen and ovate.

Hunt & DeMartini (1979) reported *V. karokorum* from 15 localities ranging from Reynolds Creek (sec. 18, T. 12 N, R. 6 E, Humboldt Base and Meridian) to Whitmore Creek (sec. 21, T. 11 N, R. 6 E). We have not reviewed their material.

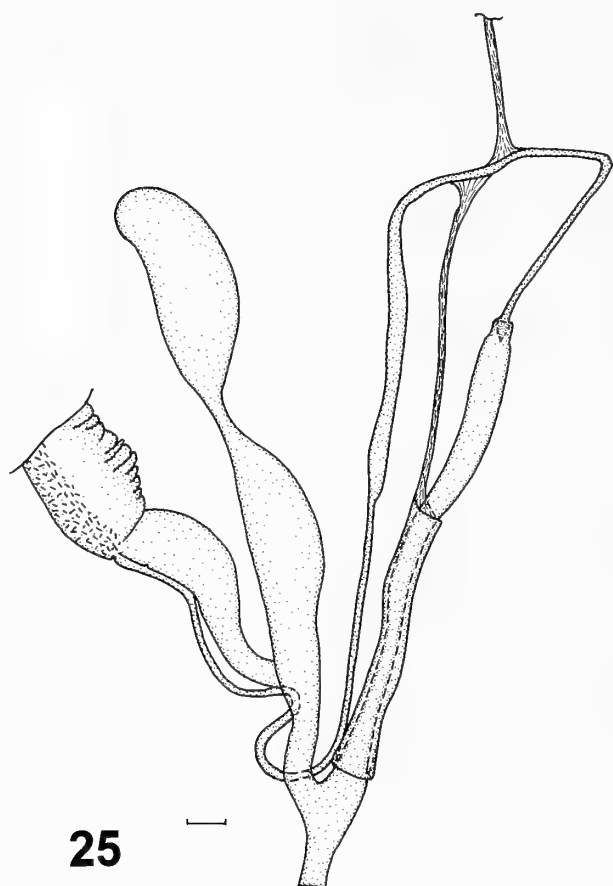
The species is found in leaf litter and under stones, branches, and debris on the ground along streams.

Vespericola klamathicus Roth & Miller, sp. nov.

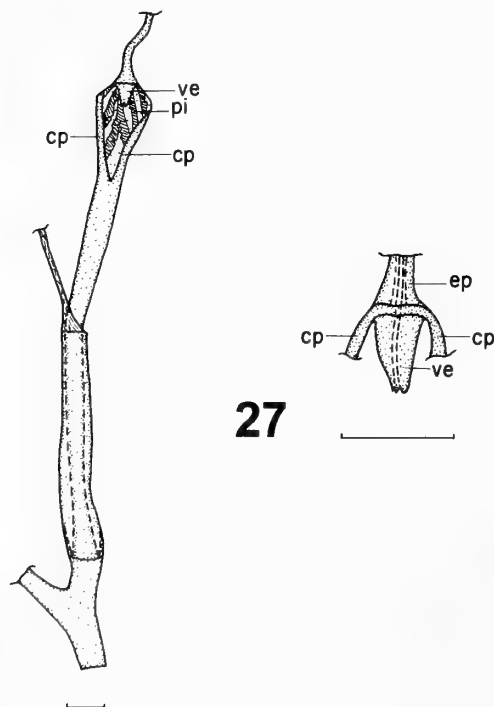
(Figures 22–27)

Diagnosis: A medium-sized to large *Vespericola* with depressed-globose, almost imperforate shell of 5.75–6.5 whorls; whorls flattened, with deeply impressed to channeled suture; periostracal setae 11–27/mm². Penis long, slender, cylindrical, containing short, conical verge with cleft tip; penial sheath covering somewhat more than half of penis.

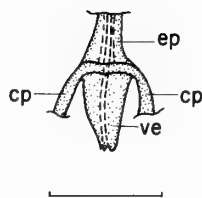
Description of shell: Shell medium-sized for the genus, depressed-globose, almost imperforate, of 5.75–6.5 whorls; base inflated, solid-looking. Spire low-domed to broadly conic, its sides weakly convex; whorls flattened; suture strongly impressed to channeled. Embryonic whorls 1.4–1.7, sculptured with low riblets radiating from suture, more or less completely broken into rows of blunt papillae. Early neanic whorls with fine, crowded, slightly retractive growth rugae and rather sparse, erect or gently curving, acicular setae in protractive, descending rows (also aligning in nearly collabral series). Periostracum between setae radially wrinkled and irregularly granulose; granules becoming obsolete on body whorl. Setae shorter, more regularly spaced, and usually closer together on subsequent whorls; 11–27 setae/mm² on body whorl. Periphery inflated, broadest above middle of whorl, somewhat sloping toward base. Base densely and regularly setose; setae smaller than on shoulder of whorl. Last whorl not markedly descending, compressed upward and sharply constricted behind lip. Aperture broadly auriculate, peristome concave in profile, oblique, at angle of about 35° to vertical; lip expanded and reflected, most strongly at base, moderately thickened submarginally. Umbilical crevice extremely narrow, oblique. Basal lip straight; inner part narrowed, slightly kinked forward, usually with low callus nodule. Inner lip dilated, nearly covering umbilicus from front. Parietal callus granulose, free edge strongly convex, swinging well to left of umbilicus, with small, rather acute sinus below upper limb of peristome. Prominent, white, triangular, convex-forward parietal lamella present. Shell light reddish brown; peristome white to pinkish tan.



25



26



27

Figures 25–27

Vespericola klamathicus Roth & Miller, sp. nov. Drawings made from projections of stained whole mounts. Scale line = 1 mm. Figure 25. Anterior part of reproductive system of holotype, SBMNH 142588, CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992. Figure 26. Penial complex of paratype, SBMNH 142589, with penis cut open to show verge and pilasters; same locality as above. Figure 27. Verge of paratype, SBMNH 142589, magnified to show cleft apex and seminal duct; same locality as above.

Dimensions of holotype: Diameter (exclusive of expanded lip) 16.0 mm, height 10.6 mm, whorls 6.25.

Measurements and counts of material at hand: Range of adult shell diameter 13.4–16.4 mm (mean of 31 specimens including holotype, 15.15 mm); height, 9.0–10.8 mm (\bar{x} = 10.11 mm); height/diameter ratio, 0.61–0.70 (\bar{x} = 0.668); number of whorls, 5.75–6.5 (\bar{x} = 6.11).

Description of soft anatomy: The holotype and five paratypes were dissected; an additional 10 specimens from nearby localities (Crawford Creek and Red Cap Gulch) also were dissected.

Living animal light tan, darker and grayer on body-stalk. Mantle over the lung clear buff, 10–30% maculated with black.

Atrium (Figure 25) of moderate length for the genus. Penis long, slender, and cylindrical, with anterior, basal half or more enclosed in thin sheath adnate to base. Penial retractor muscle inserted on the epiphallus. Narrow retentor muscle extending from penial retractor muscle at attachment on epiphallus to summit of penial sheath, from which other thin retentor fibers form connections with parts of epiphallus and vas deferens. Sheathed part of penis in holotype about 7.2 mm long; protruding part about 5.9 mm long. In paratypes, sheathed part 4.4–6.5 mm (mean 5.6 mm); protruding part 6.0–8.8 mm (mean 7.2 mm). Ratio of protruding length to sheathed length 1.0–1.7 (mean 1.32). Broad peduncular section of about 0.8 mm present between base of sheath and junction with atrium. Apex of penis containing short, conical, pointed verge 0.6 mm long and 0.4 mm wide at its base. Seminal duct opening into penial chamber at tip of verge through minute cleft about 0.1 mm long (Figure 27). Inner wall of penis with papillose, oblique pilasters.

Spermathecal duct massive, long, appressed to free oviduct (which is smaller in diameter and branches from it), elongate-ovate, about 7.0 mm long, about 1.0 mm in diameter at its junction with the oviduct, tapering gradually to 0.3 mm constriction at base of spermatheca. Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 6.0 mm long, with blunt tip.

Type material: *Holotype:* SBMNH 142588 (shell and stained whole mount of reproductive system), CALIFORNIA: Humboldt County: Aiken Creek, NE of Weitchpec, for 0.3 km upstream (west) of California Highway 96. W. B. Miller, B. Roth coll., 8 April 1992.

Paratypes: SBMNH 142589 (5 shells and stained whole mounts of reproductive system), BR 1759 (2 shells), from same locality as holotype. Additional paratypes (all, CALIFORNIA: Humboldt County:) SBMNH 78121, BR 1760, Crawford Creek, for 0.2 km upstream (north) of California Highway 96. W. B. Miller, B. Roth coll., 9 April 1992. SBMNH 78122, BR 1761, Red Cap Gulch, for 0.2 km upstream (north) of California Highway 96. W. B. Miller, B. Roth coll., 9 April 1992. Additional paratypes deposited in ANSP, CAS, LACM, and USNM.

Referred material: CALIFORNIA: Humboldt County: Pecwan (SBMNH, BR 1097); Camp Creek (BR 1863); mouth of Ullathorne Creek (CAS 052422); Ullathorne Creek (CAS 052272); Slate Creek (SBMNH); Weitchpec (SBMNH); 8.8 km S of Weitchpec (BR 956); Pull Creek (BR 1168); Mill Creek, Hoopa Valley Reservation (SBMNH).

Remarks: *Vespericola klamathicus* is distinguished anatomically from other species by its very long, slender, cylindrical penis containing a short, conical verge with a cleft tip. The genitalia most resemble those of *V. eritrichius*, but in *V. eritrichius* the tip of the verge is not cleft, the vagina is longer, and a fleshy thickening is present just below the junction of oviduct and spermathecal duct.

The high average whorl count (6.11) and flattened whorl profile with deeply impressed to channeled suture are distinctive characters of the shell of *V. klamathicus*. At the type locality, setae range from 11 to 26/mm². In all material examined, setae range from 11 to 27/mm² (mean 19.9).

Hunt & DeMartini (1979) reported "*Vespericola megasoma*" from 24 localities ranging from Blue Creek (sec. 26, T. 14 N, R. 4 E, Humboldt Base and Meridian) to the North Fork of Mill Creek (sec. 21, T. 9 N, R. 6 E). We have not reviewed this material, but much or all of it may be *V. klamathicus*.

The species is found among leaf litter and under debris on the ground along streams.

Etymology: The species is named for the Klamath Mountains. For purposes of the American Fisheries Society list of the common names of mollusks (Turgeon et al., 1988) and other administrative uses, we propose the name "Klamath hesperian."

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Zygomelon zodion, A New Genus and Species of Bathyal Volute from New Zealand

by

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Abstract. *Zygomelon zodion*, a new genus and species of Volutidae, is described from bathyal depths on the Bounty Plateau and in the Bounty Trough, southeastern New Zealand. It is referred to the tribe Alcithoini of the subfamily Zidoninae on the basis of anatomical and radular features. *Zygomelon zodion* can most easily be distinguished from species of *Alcithoe* H. & A. Adams, 1853, by the presence of two rather than four or more columellar folds. Conchological similarities between *Zygomelon* and the genus *Miomelon* Dall, 1907, of the subfamily Odontocymbiolinae lead us to hypothesize that the subfamily Odontocymbiolinae differentiated from the zidonine tribe Alcithoini in the Wedellian Province during the Paleogene.

INTRODUCTION

Deep-sea dredgings during 1979 off southeastern New Zealand yielded rich collections of mollusks, including a number of species new to science, among them the new volute described herein. With a bathymetric range of 734-1386 m, it is the deepest-living volute known from the New Zealand region. Based on features of its anatomy and radular morphology, we include this new species in the subfamily Zidoninae. However, the combination of conchological and anatomical features precludes the inclusion of this species in any genus presently known. We propose a new genus, to include this new species as well as a closely related species from the Eocene of Antarctica. Based on new morphological and paleontological data, we evaluate and expand hypotheses on the relationships and paleobiogeography of the volutid subfamilies Zidoninae and Odontocymbiolinae.

Abbreviations: NMNZ—Museum of New Zealand, Wellington; NZOI—National Institute of Water and Atmospheric Research, Wellington; USNM—National Museum of Natural History, Smithsonian Institution, Washington, DC.

SYSTEMATICS

Family Volutidae Rafinesque, 1815

Subfamily ZIDONINAE Pilsbry and Olsson, 1954

Tribe Alcithoini Pilsbry and Olsson, 1954

Zygomelon Harasewych & Marshall, gen. nov.

Type species: *Zygomelon zodion*, new species [described herein].

Diagnosis: Shell small to large (to 106 mm), stout, strongly to weakly shouldered, with prominent axial and obscure spiral sculpture. Outer lip smooth, thin. Columella with two columellar folds and siphonal fold. Siphonal fasciole weak. Operculum absent. Siphonal appendages paired, long, cylindrical. Cephalic lappets broad. Accessory salivary glands long, loosely wound around salivary glands. Radula uniserial, tricuspid, with lateral cusps broader, shorter than central cusp. Pallial sperm duct forming groove with fused edges that runs to tip of short, bluntly rounded penis.

Table 1

Zygomelon zodion Harasewych & Marshall, gen. & sp. nov. Measurement of shell and radular characters. Linear measurements in mm. $n = 4$. HT = Holotype (Figure 1), Paratype, NZOI P-957 (Figure 4), Paratype, NMNZ M.117892 (Figure 2), Paratype, NZOI P-958 (Figure 3).

	Specimen			
	HT	NZOI P-957	NMNZ M.117892	NZOI P-958
Sex	♀	♂	♀	juvenile
Shell length (SL)	50.25	43.01	28.71	9.22
Aperture length (AL)	27.92	22.70	16.42	6.17
AL/SL	0.55	0.53	0.57	0.67
Total number of whorls	6.5	6.0	5.25	2.25
Spire angle	41°	32°	40°	31°
Axial ribs body whorl	15	15	14	n/a
Axial ribs first teleoconch whorl	11	13	14	n/a
Radula length (RL)	0.14	0.14	0.12	0.09
Number of radular teeth	57	54	47	34

Etymology: *zygosis* Gr. a joining. + *melon* Gr. apple. [used as suffix for many volute genera e.g., *Adelomelon*, *Miomelon*, *Teremelon*, etc.]

Zygomelon zodion Harasewych & Marshall, sp. nov.

Figures 1–13, Table 1

Diagnosis: Shell small (to 50.2 mm), greenish tan, stout. Protoconch large, of less than two smoothly rounded whorls. Transition to teleoconch distinct. Teleoconch of up to 5¾ whorls shouldered in females, rounded in males. Eyes absent.

Description: Shell (Figures 1–4) small (to 50.2 mm), thin, biconic, with fusiform spire, rounded anterior. Protoconch (Figures 6, 7) large, of 1¾ whorls, increasing in diameter from 1.3 mm to 2.9 mm in 1¼ whorls, constricting slightly thereafter. Transition to teleoconch forming subtle but distinct varix (Figure 7, arrow). Teleoconch of up to 5¾ whorls, convex, strongly shouldered in females (Figures 1, 2), weakly shouldered in juveniles (Figure 3) and adult males (Figure 4). Suture adpressed, early whorls narrowly canaliculate. Axial sculpture of 11–15 broad, equally spaced, inflated, slightly prosocline ribs, entirely traversing early whorls, prominent on shoulder, absent along anterior portion of adult whorl. Spiral sculpture of fine spiral threads present on early whorls, obscure or absent in larger specimens. Aperture ovate. Outer lip smooth, porcellaneous, thin, not flared. Inner lip consisting of convex parietal region and axial columella with two columellar folds set obliquely to siphonal fold. Anteriormost columellar fold most pronounced, posteriormost present in juveniles, be-

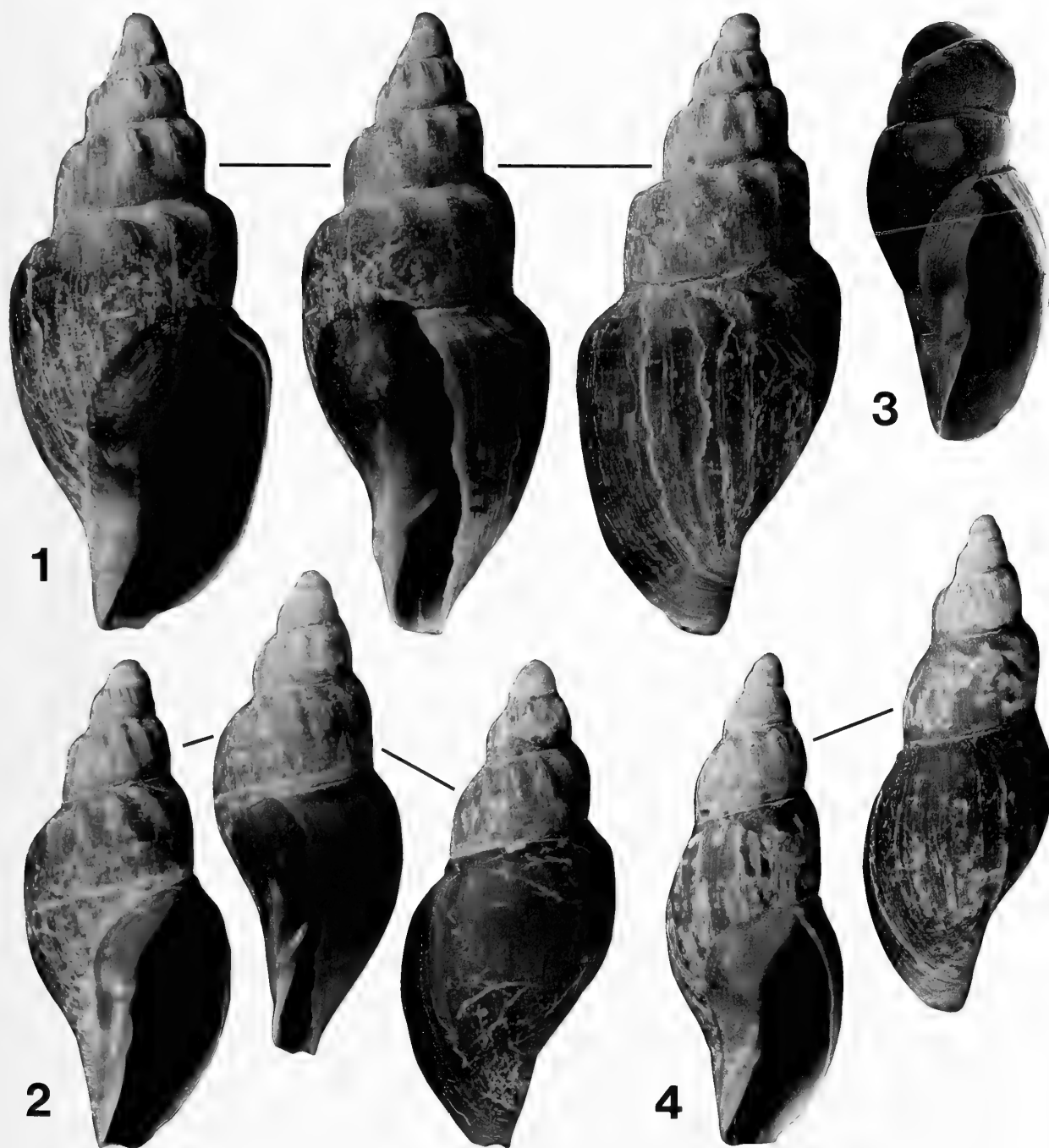
coming reduced or absent in larger specimens. Siphonal fold prominent, crossing coiling axis of shell. Surface of columella with minute pustules (Figure 5). Siphonal canal shallow, wide. Siphonal fasciole weak, inconspicuous. Periostracum thin, yellowish. Shell greenish tan. Aperture yellowish tan to brown.

External anatomy. Soft tissues comprising three whorls, mantle cavity spanning ¾ whorl, kidney ½ whorl, digestive gland and gonad 1½ whorls. Foot ($L/W \gg 2$) broad, rounded anteriorly, tapering posteriorly. Operculum absent. Animal uniformly yellowish tan. Siphon (Figure 10) short, muscular. Siphonal appendages (Figure 10, sa) paired, symmetrical, emerging from the base of the siphon and spanning half its length. Head broad, with short, tubular tentacles (Figure 10, t) flanking hood over rhynchostome. Cephalic lappets (Figure 10, cl) broad, semi-circular. Eyes absent.

Mantle cavity. Arrangement of mantle cavity organs as in *Alcithoe arabica* (Gmelin, 1791) (see Ponder, 1970). Mantle edge thin, smooth. Osphradium bipectinate, with 55 equally broad leaflets above and 48 below ganglion. Ctenidium slightly narrower, 1½ times as long as osphradium. Hypobranchial gland thin, transversely pleated, occupying dorsal midsection of mantle cavity, covering portions of the rectum and reproductive organs, producing purple secretion. Pericardium embedded in left anterior wall of kidney. Ventricle only slightly larger than auricle.

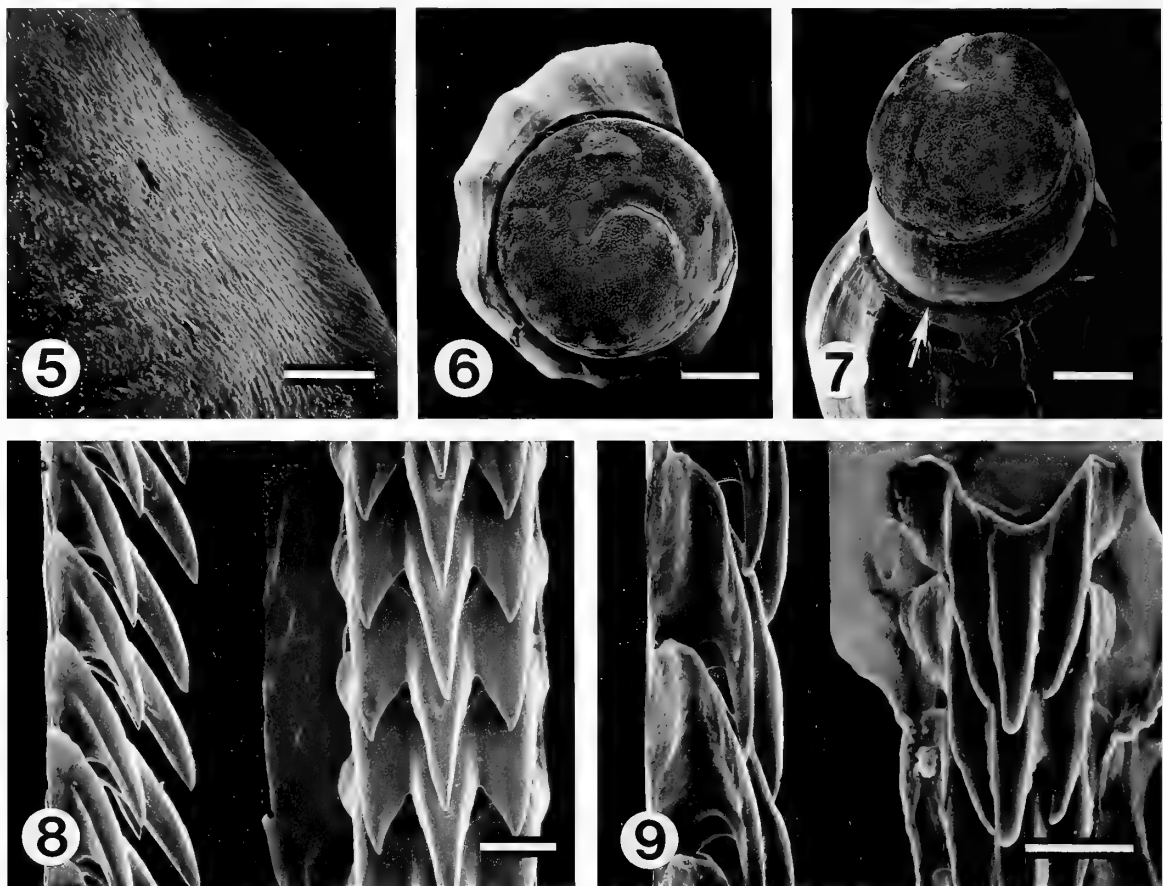
Alimentary system (Figure 11). Proboscis short, broad, extremely muscular, with retractor muscles attached to walls of cephalic hemocoel. Mouth triangular. Buccal mass small. Radular ribbon short (to 7.0 mm), uniserial, with 34–57 tricuspid teeth. Cusps broadly triangular in adults (Figure 8), joining proximally to span basal plate. Central cusp indented beneath tip of anterior adjacent tooth, lateral cusps shorter, broader than central cusp, forming slightly more acute angle with radular membrane (Figure 8). Radula of juvenile specimen (Figure 9) differing from that of adult in having cusps concentrated at midsection of basal plate, oriented nearly parallel to radular membrane. Central cusps lacking indentation, lateral cusps narrower, almost as long as central cusp. Accessory salivary glands (Figure 11, asg) tubular, convoluted, distally expanded, overlying dorsal surfaces of salivary glands (Figure 11, sg). Ducts of accessory salivary glands (Figure 11, dasg) joining prior to entering buccal cavity ventrally. Ducts of salivary glands embedded in esophagus anterior to small, indistinct valve of Leiblein (Figure 11, vl). Gland of Leiblein (Figure 11, gl) large, convoluted, filling posterior half of cephalic hemocoel. Stomach with broad, transversely pleated caecum. Intestine short, rectum (Figure 12, r) broad, rectal gland (Figure 12, rg) greenish, narrow, spanning distal third of rectum. Anus (Figure 12, a) simple.

Female reproductive system (Figure 12). Ovary whitish, lining columellar side of digestive gland. Oviduct (Figure 12, od) thin, leading from ovary to right rear corner of mantle cavity, entering anterior ventral end of large al-



Figures 1-4

Zygomelon zodion Harasewych & Marshall, gen. & sp. nov. 1. Holotype, female, NZOI H-617, Bounty Plateau, 48°30.5'S, 178°18.0'E, in 734-1012 m. $\times 1.9$. 2. Paratype, female, NMNZ M.117892, NZOI station S154, Bounty Trough, 45°24.2'S, 173°59.8'E, in 1373 m. $\times 2.7$. 3. Paratype, NZOI P-958. $\times 7.0$. 4. Paratype, NZOI P-957, male, both from NZOI station S153, Bounty Trough, 45°21.2'S, 173°35.8'E, in 1386 m. $\times 1.8$.



Figures 5-9

Zygomelon zodium Harasewych & Marshall, gen. & sp. nov. Paratype, NZOI P-958 (specimen in Figure 3). 5. Columella adjacent to anteriormost fold. Scale bar = 100 μ m. 6. Apical and 7. oblique views of protoconch. Arrow denotes varix at transition to teleoconch. Scale bars = 50 μ m. 8. Lateral and dorsal views of radula of the holotype (Figure 1). Scale bar = 100 μ m. 9. Lateral and dorsal views of radula of juvenile specimen in Figure 3 (paratype, NZOI P-958). Scale bar = 100 μ m.

bumen gland (Figure 12, ag) adjacent to right ventral kidney wall. Ingesting gland (Figure 12, ig) joining pallial oviduct at rear of the mantle cavity. Capsule gland (Figure 12, cg) short, broad, enveloped, together with rectum, rectal gland, in connective tissue and muscular sheath. Capsule gland joining nearly spherical bursa copulatrix (Figure 12, bc), with female opening (Figure 12, fo) at anteriormost end.

Male reproductive system. Testes lining inner edge of digestive gland, emptying through tubular duct passing along pericardium prior to entering mantle cavity and expanding to form prostate gland. Prostate gland broader, slightly shorter than penis, opening to mantle cavity via ventral slit. Pallial vas deferens tubular, running anteriorly along mantle cavity wall, forming groove with fused edges upon descending to mantle cavity floor. Groove extending to base of penis. Penis (Figure 10, p) short ($< \frac{1}{2}$ mantle cavity length), ovate in section, tapering gradually to blunt-

ly rounded distal end. Penial duct (Figure 10, pd), a fused slit, running along inner edge of penis from base to tip.

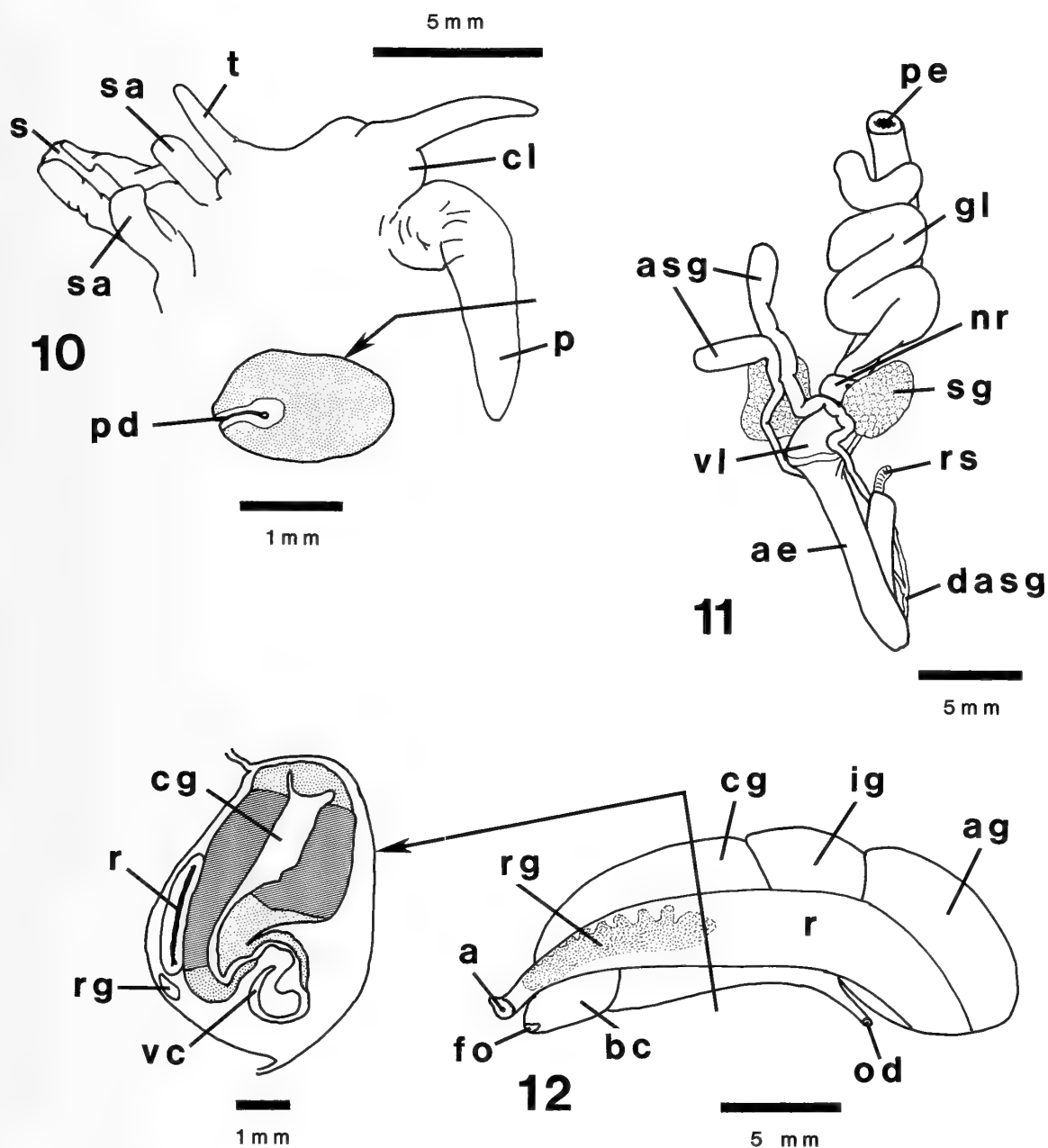
Kidney. Kidney large, typical of volutids as exemplified by *Alcithoe arabica* (see Ponder, 1970:fig. 33). Nephridial gland, adjacent to the pericardium, comprising approximately $\frac{1}{3}$ kidney width.

Nervous system. Supraesophageal and right pleural ganglia fused, corresponding to nervous system type 2 (Ponder, 1970:159).

Etymology: *zodium* Gr.—a small animal.

Type locality: Bounty Plateau, southeastern New Zealand, 48°30.5'S, 178°18.0'E, 734–1012 m, NZOI stn I697, 19 March 1979.

Material examined: Holotype, female, NZOI H-617, from the type locality. Paratypes (2), NMNZ M.117892, Paratypes (2), NZOI P-955,956, Paratype, USNM



Figures 10-12

Zygamelon zodion Harasewych & Marshall, gen. & sp. nov. 10. Dorsal view of head and penis, with siphon reflected to left. 11. Anterior alimentary system. 12. Female glandular oviduct. Key: a, anus; ae, anterior esophagus; ag, albumen gland; asg, accessory salivary gland; bc, bursa copulatrix; cg, capsule gland; cl, cephalic lappet; dasg, duct accessory salivary gland; fo, female opening; gl, gland of Leiblein; ig, ingesting gland; nr, nerve ring; od, oviduct; p, penis; pd, penial duct; pe, posterior esophagus; r, rectum; rg, rectal gland; rs, radular sac; s, siphon; sa, siphonal appendage; sg, salivary gland; t, tentacle; vc, ventral channel; vl, valve of Leiblein.

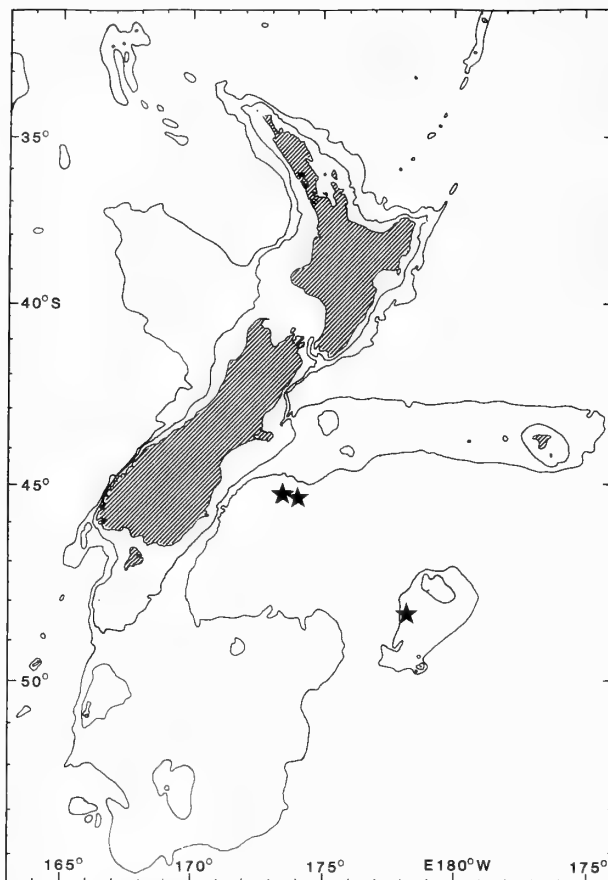


Figure 13

Map of New Zealand region showing distribution (stars) of *Zygomelon zodium* Harasewych & Marshall, gen. & sp. nov. 200 and 1000 m contours indicated.

860379, Bounty Trough, 45°24.2'S, 173°59.8'E, 1373 m. NZOI stn. S154, 27 October 1979. Paratype, male, NZOI P-957, Paratypes (2), juveniles, NZOI P-958, Bounty Trough, 45°21.2'S, 173°35.8'E, 1386 m, NZOI stn. S153, 27 November 1979.

Distribution: (Figure 10). This new species is known at present from three stations on the Bounty Plateau and in the Bounty Trough. The bathymetric range is 734–1386 m.

Comparative remarks: The shell of *Zygomelon zodium* most closely resembles that of the odontocymbioline volutes *Miomelon eltanini* Dell, 1990, which ranges from the Falkland Islands to the Bellinghausen Sea at depths of 646–1971 m, and *Miomelon philippiana* (Dall, 1890) from comparable depths off the coast of Chile. There is a particularly close correspondence in the morphology of the protoconchs of these species as well as in the number and relative prominence of their columellar folds. However, *Zygomelon zodium* cannot be included in *Miomelon* as it is clearly referable to the subfamily Zidoninae, lacking the

following features that have been reported in all species of Odontocymbiolinae studied to date: a “fanglike” radula with well-separated cusps that emerge from anterior margins of rectangular basal plates; a stomach with a broad, tubular anterior region; accessory salivary glands that are intertwined with and embedded in the salivary glands; and a penis with a terminal papilla (Harasewych, 1987:7).

Of the Recent (Weaver & du Pont, 1970; Powell, 1979; Poppe & Goto, 1992) and fossil (Beu & Maxwell, 1990) New Zealand volutes, *Zygomelon zodium* is superficially similar to species of the genus *Alcithoe*, especially small forms of *Alcithoe wilsonae* (Powell, 1933), but it lacks the four strong, oblique columellar folds characteristic of that genus. Although it differs from *Zygomelon zodium*, in having a proportionally larger aperture, *Pachymelon* (*Palomelon*) *suropsilos* Stilwell & Zinsmeister, 1992, from the late Eocene of Seymour Island, Antarctica, is similar in that it “reveals slight evidence of two columellar folds” (Stilwell & Zinsmeister, 1992:145). The presence of two columellar folds precludes the inclusion of *P. suropsilos* in *Pachymelon* Marwick, 1926 (Type species: *Waihaioa amoriaformis* Marwick, 1926; Early Miocene, New Zealand), and indicates that it is more appropriately assigned to *Zygomelon*. The type species of *Palomelon* Finlay, 1926 (*Cymbiola lutea* Watson, 1882; Recent, New Zealand) is a typical *Alcithoe* species, and we follow Dell (1978) in treating this subgenus as a synonym of *Alcithoe*.

DISCUSSION

In their revision of the family Volutidae, Pilsbry & Olsson (1954) erected the subfamily Alcithoinae, further subdividing it into the tribes Alcithoini, Pachycymbiolini, and Zidonini (as Alcithoides, Pachycymbiolides, and Zidonides respectively). As originally proposed, Alcithoini contained Recent and fossil genera from Australia, New Zealand, and India; the Pachycymbiolini were restricted to South America and the eastern Pacific, whereas Zidonini comprised a single monotypic genus from the southern Atlantic. Clench & Turner (1964:147) pointed out that Zidoninae H. & A. Adams, 1853 was a senior synonym of Alcithoinae, as both contained the genus *Zidona* H. & A. Adams, 1853. They did not modify the concept of the subfamily other than to expand its characterization to include a number of anatomical features. In their classification of the caenogastropods, Ponder & Warén (1988: 306) listed the subfamily Alcithoinae as separate from the Zidoninae, without discussion.

Apart from the geographic separation, the primary differences between Alcithoini and Pachycymbiolini appear to be in early development. The protoconchs of species of Alcithoini have a “relatively large nucleus, often high or elevated, but composed of a few whorls, of which the initial one is already quite large” (Pilsbry & Olsson, 1954:281). The protoconchs of Pachycymbiolini, on the other hand, usually have bulbous, secondarily calcified whorls with pointed calcarella (Clench & Turner, 1964:136). Both

groups have large, nearly spherical egg capsules, although calcified egg capsules have been reported only in Alcithoini (Powell, 1979:211).

Early whorls of Zidonini are small, lack a calcarella, and are covered by a spinelike callus. Animals have an enlarged left mantle lobe that completely envelopes the shell and produces a microscopically pustulated overglaze on the outer surface of the shell. Although the tribe originally contained only the geographically restricted, monotypic genus *Zidona*, species of *Iredalina* Finlay, 1926, and *Provocator* Watson, 1882, also share these features and extend the range of the tribe throughout the Southern Ocean.

On the basis of anatomical similarities, Harasewych (1987:8) suggested that the Odontocymbiolinae was derived from the Zidoninae, and that the two subfamilies are closely related. The conchological similarities between *Zygomelon* and *Miomelon*, a genus within Odontocymbiolinae, lead us to further restrict the ancestor of Odontocymbiolinae to the tribe Alcithoini, either to *Zygomelon* or to a closely related genus.

The zoogeographic hypothesis that Odontocymbiolinae radiated in the Wedellian Province during the Paleogene (Harasewych, 1987:8) is supported by the finding of a progenitor of *Miomelon* in the Late Eocene-Early Oligocene of Seymour Island. The geographic distribution of the Pachycymbiolini suggests that this group also radiated in the Weddellian Province (Zinsmeister, 1979, 1982) after the separation of New Zealand at the end of the Early Paleocene. Inferences about the age and biogeography of Zidonini must await clarification of the relationships between *Zidona*, *Provocator* and *Iredalina*.

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Corrections to Type Locality and Geographic Range for Three Species of Australasian Volutes (Volutidae: Amoriinae and Zidoninae)

by

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Abstract. The recent discovery of living specimens of *Amoria spenceriana* (Gatliff, 1908) has revealed the type locality to be erroneous. The species is restricted to Ashmore Reef in the central western sector of the Timor Sea. *Cymbiola cymbiola* (Gmelin, 1791), another tropical species, has a much more extensive range in the Timor and Arafura Seas than was previously appreciated. Taxonomic uncertainties resulting from hitherto accepted geographical distributions are rectified for both species. The holotype of *Voluta rossiteri* Brazier, 1898, the only known specimen, supposedly from Lakes Entrance, eastern Victoria, is a worn specimen of the New Zealand species *Alcithoe arabica* (Gmelin, 1791).

INTRODUCTION

"No shell is really rare; we simply have not been able to locate its habitat" (quotation by C. M. Burgess in Leehman, 1975). This statement is particularly apt for the two tropical species of volutes discussed in this paper, *Amoria spenceriana* (Gatliff, 1908) and *Cymbiola cymbiola* (Gmelin, 1791), both of which are generally considered very rare. In reality, both species are probably common, but their distributions have been wrongly cited. The true identity of the third species, *Voluta rossiteri* Brazier, 1898, has long been an enigma. This paper shows that the correct taxonomic status of all three species becomes much clearer when their correct geographic range is recognized. The increase in our knowledge of these volutes has come about not only through additional sampling in Australasian coastal waters, but also the unstinting work of discerning amateur collectors keen to know more about supposedly rare species. Commensurate with the establishment of the valid name and determination of the geographical limits comes the onus for conservation when, as is the case of one of the species dealt with here, the range turns out to be very restricted.

TAXONOMY

Amoria spenceriana (Gatliff, 1908)

(Figures 1-7)

Voluta (Amoria) spenceriana Gatliff, 1908:84, pl. 4.

Scaphella spenceriana (Gatliff): Hedley, 1910:362.

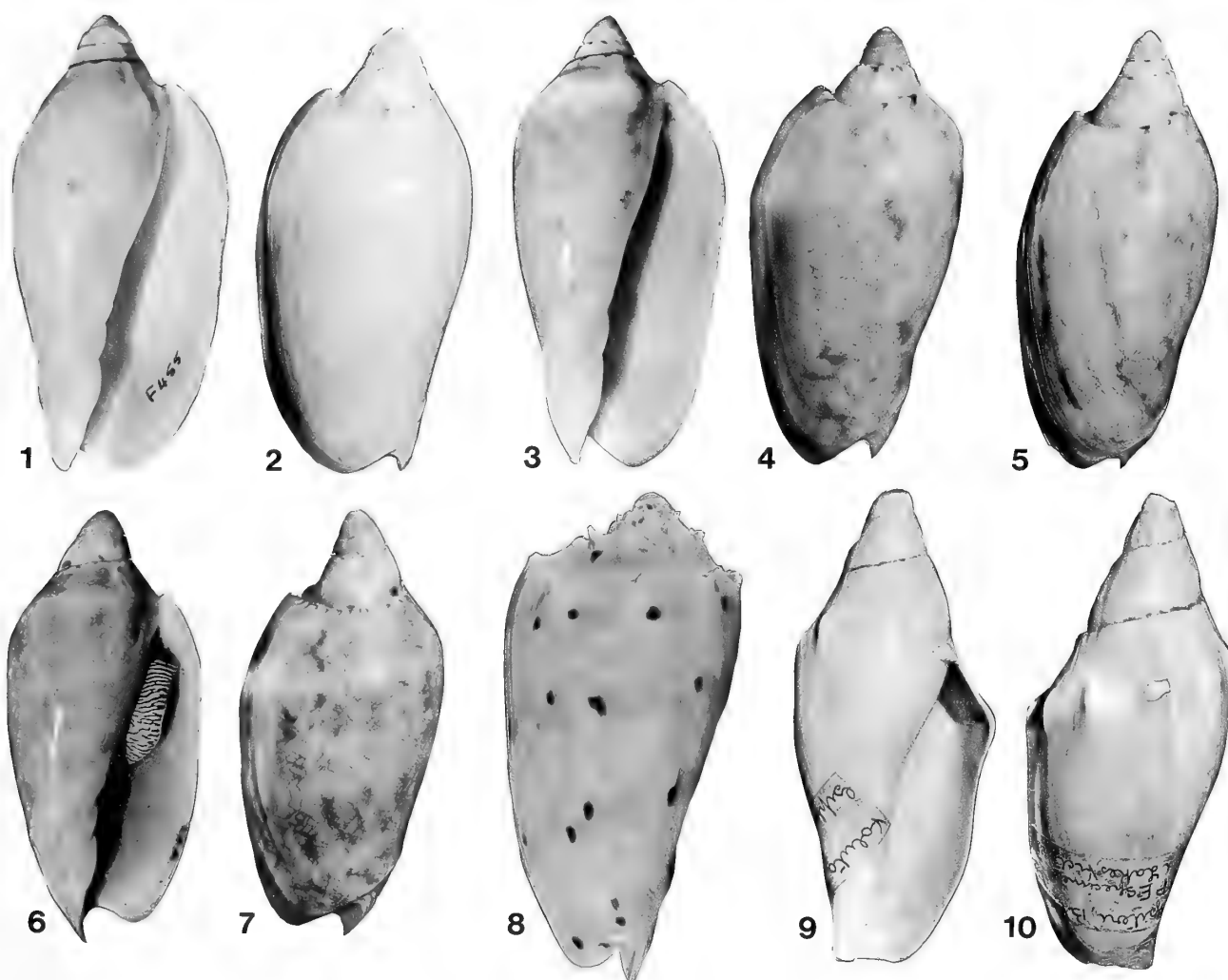
Amoria spenceriana (Gatliff): M. Smith, 1942:54, pl. 25, fig. 176; Rippingale & McMichael, 1961:116, pl. 15, fig. 16.

Amoria (Amoria) spenceriana (Gatliff): Ludbrook, 1953:141-142, pl. 18, figs. 7, 8; Weaver & du Pont, 1970:157-158, pl. 65I, J.

Amoria praetexta (Reeve): Wells, 1993:36; Wilson, 1994:113, pl. 19, fig. 3A (non *Voluta praetexta* Reeve, 1849).

Amoria maculata (Swainson): Wilson, 1994:pl. 20, fig. 1E (holotype of *Voluta (Amoria) spenceriana* Gatliff) (non *Voluta maculata* Swainson, 1822).

Material examined: Holotype, 55.1 mm, "North Queensland," Gatliff Collection, National Museum of Victoria, Melbourne, Registered number F455. 2 specimens, 61.2, 43.3 mm, live-taken, on low-tidal sand bank, Ashmore Reef, Timor Sea, September 1985, J. Clark collection. 3 specimens, 60.0, 57.8, 47.6 mm, taken dead on clean sand, in the lagoon, Ashmore Reef, Timor Sea, September 1985, J. Clark collection. 2 specimens, 65.3, 56.8 mm, on exposed coral reef, 10 meters depth, Ashmore Reef, Timor Sea, 24 September 1985, H. Morrison collection. 1 specimen, 65.3 mm, dead on sandflat off West Islet, Ashmore Reef, Timor Sea, 11 September 1986, Western Australian Museum, Perth, Registered number WAM 10-94. 1 specimen, 59.0 mm, dead on lagoon bommie, northern side of Ashmore Reef, Timor Sea, 14 September 1986, Western Australian Museum, Perth, Registered number WAM 9-94. 1 specimen, 61.2 mm, fresh crabbed, on a sandbank on the lagoon, N.E. Ashmore Reef, Timor Sea, 15 September 1986, Western Australian Museum, Perth, Registered number WAM 8-94. 1 specimen, 54.5 mm, dead on reef flat north



Explanation of Figures 1 to 10

Figures 1 to 7. *Amoria spenceriana* (Gatliff). Figures 1, 2. Holotype, 55.1 mm, "North Queensland" (sic, type locality herein corrected to Ashmore Reef, Timor Sea), NMV F455. Figures 3, 4. 61.2 mm, live-taken, on low-tidal sandbank, Ashmore Reef, Timor Sea, J. Clark collection. Figure 5. 66.6 mm, in beach drift, West Islet, Ashmore Reef, Timor Sea, NTM P16205. Figures 6, 7. 60.1 mm, live-taken on rubble at night, 3 meters depth, Central Passage, between North and Middle Islets, Ashmore Reef, Timor Sea, H. Morrison collection. Figure 8. *Cymbiola cymbiola* (Gmelin). 82.1 mm, 10 meters depth, southwest of Booby Island, Gulf of Carpentaria, NTM P16070. Figures 9, 10. *Voluta rossiteri* Brazier. Holotype, 108.0 mm, "Gippsland Lakes Entrance, Victoria" (sic, herein corrected to New Zealand), SAM D8322.

of West Islet, Ashmore Reef, Timor Sea, 17 September 1986, Western Australian Museum, Perth, Registered number WAM 11-94. 1 specimen, 57.3 mm, in beach drift, West Islet, Ashmore Reef, Timor Sea, 8 October 1992, H. Morrison collection. 2 specimens, 60.1, 56.6 mm, crawling on rubble at night and dead shell respectively, 3 meters depth, Central Passage, between North and Middle Islets, Ashmore Reef, Timor Sea, 9 October 1990, H. Morrison collection. 1 specimen, 56.5 mm, taken dead amongst coral rubble, 20 meters depth, N.E. corner of Ashmore Reef, Timor Sea, 5 October 1992, A. Limpus

collection, Registered number 00 999. 1 specimen, 51.1 mm, taken dead amongst coral rubble, 20 meters depth, N.E. corner of Ashmore Reef, Timor Sea, 6 October 1992, H. Morrison collection. 1 specimen, 66.6 mm, in beach drift, West Islet, Ashmore Reef, Timor Sea, November 1992, Museum and Art Gallery of the Northern Territory, Darwin, Registered number P16205.

Remarks: *Amoria spenceriana* (Gatliff, 1908) belongs to a group of 10 nominal *Amoria* species, all sharing black flashes on the ramp immediately below the suture of the

shell, red radial lines on the head-foot, and (about 10) broad red rings around the siphon of the animal (good illustrations of this type of pigmentation are provided for *A. maculata* (Swainson, 1822) by Weaver & du Pont (1970: pl. 70, bottom photograph) and by Coucom (1991:1, unnumbered middle photograph)). These species are *A. spenceriana*, *A. maculata*, *A. damonii* Gray, 1864, *A. grayi* Ludbrook, 1953, *A. jamrachi* Gray, 1864, *A. diamantina* Wilson, 1972, *A. keatsiana* Ludbrook, 1953, *A. reticulata* (Reeve, 1844), *A. praetexta* (Reeve, 1849), and *A. turneri* (Griffith & Pidgeon, 1834). Two subsets are recognizable within this group on the basis of shell and animal pigmentation. *Amoria spenceriana* belongs to the smaller one containing only it plus *A. maculata* and *A. praetexta*. All three species possess spiral rows of brown blotches on the shell and (about five) red rings around the tentacles of the animal. *A. spenceriana* and *A. praetexta* share a tented pattern with each other and with most species in the other group. *A. spenceriana* is relatively broad, with a short spire and particularly expanded body whorl; it develops an extended spiral channel (Abbottsmith, 1969:81), and the outer lip sweeps upward adapically where it touches the penultimate whorl in fully grown shells; it has only three columellar plaits (there are four in one exceptional specimen, but in that shell (P16205), the adapical plait is very weak and obviously bifid), its siphonal canal is relatively deep, its ground coloration is off-white or light cream, its axial markings consist of vague and narrow, brown flares, its tenting is weakly developed, appearing most strongly only in the vicinity of the shoulder, and the interior of the aperture is flesh pink when live, fading to white after death. *A. praetexta* is relatively more slender without any noticeable expansion of the whorls; the outer lip follows the existing sutural contour without sweeping upward in fully adult shells; it has four columellar plaits (74%, $n = 19$) more frequently than three; its ground coloration is cream; its shell is conspicuously tented all over, rendering it rather dark at first impression, the black flashes on the presutural ramp are very numerous; darker zig-zags are incorporated into the tenting as two indefinite zones around the center of the shell; and the interior of the aperture is chestnut brown when live. Abbottsmith (1969:25) illustrated the color forms known to occur in *A. praetexta*. *A. maculata* is relatively broad and the shell has a distinct shoulder, it consistently has four columellar plaits, its siphonal canal is relatively shallow, its ground coloration is cream to tan, its axial markings consist of four rows of strong broad brown elongate blotches (Abbottsmith, 1969:23, 24 illustrated the various patterns that these markings can take), there is never any tenting, and the interior of the aperture is cream to tan depending on the color of the exterior.

Gatliff (1908) supplied only the imprecise type locality "North Queensland" when he described *Voluta* (*Amoria*) *spenceriana*. Weaver & du Pont (1970:pl. 65I, J) figured a shell matching the holotype, but its locality was uncertain. Poppe & Goto (1992:198) used the name for a deep-

water form of *A. maculata* from northern Queensland (the "Corbett Reef form" of Abbottsmith, 1969:26). Wilson (1994:112) has gone so far as to list *A. spenceriana* as a synonym of *A. maculata*, presumably because of the type locality.

Although no specimens corresponding to the holotype have been taken in northeastern Australian waters in the 87 years since Gatliff described *Amoria spenceriana* (personal observation; personal communication, A. Limpus), 17 specimens identical to it have come to my attention from one coral reef in the Timor Sea off northern Western Australia. This reef is Ashmore (12°17'S, 123°02'E), a raised platform reef on the outer edge of the Australian Continental (Sahul) Shelf approximately midway between the Kimberley coast and the Indonesian island of Timor. Ashmore Reef, which is 30 km long and 239 km² in area, actually encloses a complex of patch reefs, sand banks, (three) emergent cays and (two) lagoons (Russell & Vail, 1988; Vail & Russell, 1989; Wells, 1993). *A. spenceriana* is apparently not rare on Ashmore Reef, as most visits there over the last decade have yielded some specimens. Their true identity has gone unrecognized because they were misidentified as *A. praetexta* (e.g., Wells, 1993; Wilson, 1994).

Two smaller coral reefs lie on the outer edge of the Shelf adjacent to Ashmore Reef—Cartier Reef (12°32'S, 123°33'E), 61 km to the southeast, and Hibernia Reef (11°58'S, 123°22'E), 25 km to the northeast. The molluscan faunas of both reefs were sampled by the author as part of a biological survey conducted by the Museum and Art Gallery of the Northern Territory in 1992 (Willan, 1993), and no specimens of *Amoria spenceriana* were found. Neither does *A. spenceriana* occur on Seringapatam Reef (13°41'S, 122°05'E), Scott Reef (14°0'S, 121°45'E), or the Rowley Shoals (17°10'S, 119°20'E), coral atolls rising from the Continental Slope several hundred kilometers farther south of Ashmore Reef (Wells, 1983; Wells & Slack-Smith, 1986).

Recognition that Ashmore Reef is the only place where *Amoria spenceriana* lives necessitates a correction of the type locality. Furthermore, it gives this species the distinction of being the most narrowly restricted of all Australia's volutes. Ashmore Reef has been declared an Australian National Nature Reserve since 1983, principally to protect nesting turtles and sea birds. The discovery of a distinctive, endemic gastropod adds significantly to its conservation value.

Cymbiola cymbiola (Gmelin, 1791)

(Figure 8)

Voluta cymbiola Gmelin, 1791:3468; Reeve, 1849: *Voluta* species 46, pl. 19, fig. 46; Poppe, 1982:10.

Voluta corona Dillwyn, 1817:576; Kiener, 1839:49, 50, pl. 41, fig. 1; Sowerby, 1845:193, pl. 55, figs. 120, 121.

Voluta flammulata Wood, 1828:10.

Voluta cymbiola Sowerby (= error pro. Gmelin): Tryon, 1882: 99, pl. 29, figs. 118, 119.

Aulica cymbiola (Chemnitz): M. Smith, 1942:35, pl. 17, fig. 113.

Cymbiola (*Cymbiola*) *cymbiola* (Chemnitz): Wenz, 1943:1334, 1335, text fig. 3788; Weaver & du Pont, 1970:76, pls. 38A–C; Poppe & Goto, 1992:158, pl. 64, figs. 1–3; Dharma, 1992:54, pl. 5, figs. 4, 4a, 4b.

Voluta (*Cymbiola*) *cymbiola* Gmelin: Leehman, 1975:12; Leehman, 1981:12.

Cymbiola cymbiola (Gmelin): Pel, 1976:4; Darragh, 1989: 260; Whitehead & Potter, 1993:1, 2; Loch, 1993:6; Wilson 1994:120, pl. 17, figs. 4a–b.

Material Examined: GULF OF CARPENTARIA—1 specimen, 82.1 mm, dredged in substrate of sand, seagrass and algae, 10 meters depth, southwest of Booby Island, NE section, Gulf of Carpentaria, R. S. Williams on R. V. "Southern Surveyor," 29 November 1991, Museum and Art Gallery of the Northern Territory, Darwin, Registered number P16070. 1 specimen, 49.6 mm, trawled 54 meters depth, central section, Gulf of Carpentaria—13°03.7'S, 138°47.4'E, 24 November 1991, A. Limpus collection, Bundaberg. 1 specimen, 62.0 mm, trawled, 55 meters depth, near Groote Eylandt, NW section, Gulf of Carpentaria, 1986, A. Klishans collection, Darwin. ARAFURA SEA—2 specimens, 64.3, 62.0 mm, trawled off Aru Island, A. Limpus collection, Bundaberg. 3 specimens, 59.7, 58.0, 57.0 mm, low tide, Tanimbar, Moluccas Islands, A. Limpus collection, Bundaberg. TIMOR SEA—3 specimens, 76.8, 67.7, 42.1 mm, trawled in deep water, Timor Sea, Bellview Shell Collection. 2 specimens, 84.6, 69.5 mm, Joseph Bonaparte Gulf, northwestern Australia, H. Morrison collection, Perth. 2 specimens, 81.0, 75.5 mm, trawled off the Kimberley coast, northwestern Australia, S. Marshall collection, Augusta Shell Museum. 1 specimen, 63.4 mm, taken by Taiwanese trawling vessel, off Dampier, northwestern Australia, A. Limpus collection, Bundaberg. 1 specimen, 68.0 mm, trawled 400–500 meters depth, northwest of Port Hedland, A. Limpus collection, Bundaberg. FLORES SEA—1 specimen, 61.4 mm, trawled 10.6 meters depth, off Flores Island, T. Gabelish collection, Perth. JAVA SEA—2 specimens, 73.0, 67.0 mm, dredged in substrate of mud, 40 meters depth, approximately 370 km east of Bali, Indonesia, 1974, A. Klishans collection, Darwin. PROVENANCE UNCERTAIN—1 specimen, 89.9 mm, Purchased in Taiwan with probable locality "Arafura Sea," A. Limpus collection, Bundaberg. 1 specimen, 66.0 mm, "North West Australia, 7 August 1986," J. W. Oakman collection, Darwin. 1 specimen, 68.4 mm, trawled "Indonesia," A. Limpus collection, Bundaberg.

Remarks: *Cymbiola cymbiola* (Gmelin, 1791) is the type species of the zidonid genus *Cymbiola* Swainson, 1831. Although most authors have generally considered that it was a distinct species, its status came into question 20 years ago. At that time, some raised the possibility that it was consubspecific with *C. sophia* (Gray, 1846) or that the

two were forms of the same species (Leehman, 1975). This uncertainty stemmed from the paucity of specimens then available for study. With the discovery of considerable numbers of specimens in recent years (Leehman, 1981; Poppe, 1982), a set of constant characters has emerged by which *C. cymbiola* can be distinguished from the partially sympatric *C. sophia*. These characters are the smooth protoconch of *C. cymbiola* (ribbed in *C. sophia*), the narrower and more elongate shape of *C. cymbiola*, and presence of two additional adapical columellar plaits in the adult specimens of *C. cymbiola* (Poppe, 1982; Whitehead & Potter, 1993).

Twenty years ago, there were so few specimens of *Cymbiola cymbiola* known that Weaver & du Pont (1970:76) could write: "It is doubtful if any specimens of *Cymbiola cymbiola*, dead or living, have been collected in this century." In those days, the discovery of a shell in an old collection was something to publicize (Pel, 1976). Searches for this species were then directed in the vicinity of the Banda Sea, particularly around the central Moluccas Islands under the assumption that the species could be found there. That belief stemmed from Reeve (1849), who stated "Moluccas" in *Conchologia Iconica*, but it has been put into doubt by the recent discovery of numerous live specimens from further south (Leehman, 1981; Poppe, 1982). Seven shells, including the one illustrated here in Figure 8, were taken during fisheries research cruises in the Gulf of Carpentaria in 1990 and 1991 (Whitehead & Potter, 1993; Loch, 1993), so that the eastern limit of the range is now established at approximately 142°E. Wilson (1994) cites the western limit at Joseph Bonaparte Gulf, Western Australia. The northwestern, and especially northern, limits of distribution remain confused because of the peregrine activities of the Asian trawling fleet. Wilson (1971) authenticated the existence of the species in the vicinity of the Aru Islands in the northern Arafura Sea, but whether *C. cymbiola* actually extends farther north through the Banda Sea to the Moluccas Islands still awaits confirmation. Assuming *C. cymbiola* is a shallow-water species with direct development, like other species of *Cymbiola* (personal observation), its range could well be circumscribed by deep ocean barriers, notably the Coral Sea Basin to the east, the South Banda Basin and Savu Basin to the northwest, and the North Australian Basin to the west.

Voluta rossiteri Brazier, 1898

(Figures 9, 10)

Voluta rossiteri Brazier, 1898:779, 780; Iredale, 1958:118; Darragh, 1989:217, 222, pl. 5, figs. 1, 7.

Notovoluta rossiteri (Brazier): Cotton, 1946: 16; Cotton, 1949: 194; Abbottsmith, 1969:81; Wilson, 1972:348.

Notovoluta rossiterie (sic = error pro. *rossiteri*) (Brazier): Weaver & du Pont, 1970:168, 169, pls. 72F, G.

Material examined: Holotype, 84.0 mm (not 108.00 mm as stated by Brazier, 1898), "Gippsland Lakes Entrance,

Victoria," Kenyon Collection, South Australian Museum, Adelaide, Registered number D8322.

Remarks: The holotype is a very worn shell. Only $3\frac{1}{2}$ (not six as stated by Brazier, 1898) teleoconch whorls are present. The apical whorl is infilled with hard, transparent material. The third whorl has 18 close, broad, flattened (due to postmortem erosion), axial ribs that extend from suture to suture, but there are no spiral threads. The body whorl has 10 well-spaced, weak, rounded tubercles on the shoulder. The suture is irregular. The outer lip and siphonal canal are extensively damaged. The shell is cream (actually much paler than shown by Weaver & du Pont, 1970) with faint, orange, transverse zig-zag markings on the body whorl. There are four, thin yet strong, oblique columellar plaits.

This shell belongs to the zidonid genus *Alcithoe* H. & A. Adams, 1853 because of its fusiform shape, axial ribbing on the teleoconch whorls, form of the columellar plaits, and coloration. No species of this genus exists in the Recent Australian fauna, and this shell does not correspond with any of the nine fossil taxa described by Darragh (1989) from southeastern Australia, except its shape is like that of *A. pueblensis* (Pritchard, 1898) and *A. neglectoides* Darragh, 1989. However, both these species have numerous, close-set spiral threads covering the spire whorls and, in the latter species, the entire body whorl too. The holotype of *Voluta rossiteri* is in fact a long dead specimen of *Alcithoe arabica* (Gmelin, 1791), that was almost certainly found on a beach. *A. arabica* is endemic to New Zealand, so the shell must have originated from that country. It belongs to the form called *swainsoni* Marwick, 1926 on account of its particular shape and well-separated, elongate, relatively weak, axially aligned tubercles on the shoulder of the body whorl.

The South Australian Museum has little record of the origin of the shell. Mrs. Agnes F. Kenyon of Melbourne loaned it to John Brazier to name. Not being much of a field collector herself, Mrs. Kenyon bought specimens from dealers and exchanged with other collectors (R. Burn, personal communication, 1994). Sir Joseph Verco purchased the Kenyon collection and donated it to the South Australian Museum (K. Gowlett-Holmes, personal communication, 1994). Discussions with colleagues versed in historical malacology in New South Wales, Victoria, and South Australia offered no firm explanation as to why Brazier believed this shell came from Australia. Brazier was usually very reliable with locality data (I. Loch, personal communication, 1994), so this advice came from either Mrs. Kenyon or Richard C. Rossiter.

In all probability, Wilson (1972) accepted the authenticity of Brazier's Australian locality when he concluded that *Voluta rossiteri* was a junior synonym of *Notovoluta kreuslerae* (Angas, 1865). He, like Darragh (1989:222), who maintained the synonymy, may not have been aware of the enormous intraspecific variability of *Alcithoe arabica* in New Zealand waters. *Notovoluta kreuslerae* has a shorter

and more solid shell with stronger shoulder tubercles; microscopic spiral striations are present above the shoulder on the spire whorls, and it has a closely tented color pattern. This Australian species extends from off Hopetoun, southern Western Australia, to off Cape Otway, central Victoria, on the mainland and western Bass Strait (Burn, 1983), but it does not reach Lakes Entrance in eastern Victoria (C. Griffiths, personal communication, 1994). Currently shell collectors are (mis)applying the name *Notovoluta rossiteri* to any form of *N. kreuslerae* that occurs east of Fleurieu Peninsula, South Australia (for example see Limpus, 1992, unnumbered middle photograph).

ACKNOWLEDGMENTS

Allan Limpus of Bundaberg has been as keen as I have been to resolve the taxonomy and geographical range of these three enigmatic species. He generously allowed me to examine his extensive collection of volutes and offered many helpful suggestions. During his travels around Australia he consulted Coralie Griffiths and Barry Hutchins in relation to this study. The following people kindly made specimens available to Allan and myself: Clay Bryce, Chris Rowley, Hugh Morrison, and John Clark (*Amoria spenceriana*), Tony Gabelish, Alan Klishans, Steve Marshall, Hugh Morrison, John Oakman, and Frank Wong (*Cymbiola cymbiola*), and C. S. Lee and Karen Gowlett-Holmes (holotype of *Voluta rossiteri*). I am grateful to Karen as well as Robert Burn and Ian Loch for discussions on the history of the holotype of *Voluta rossiteri*.

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A Second Species of *Haustellotyphis* (Gastropoda: Typhidae) from Costa Rica

by

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Abstract. A new species, *Haustellotyphis wendita*, superficially resembling *Haustellotyphis cumingii* (Broderip, 1833), but with differences in protoconch characters and subtle sculptural details is described from the Pacific coast of Costa Rica. The new species is compared with *H. cumingii*, and SEM photographs of the radulae are shown.

INTRODUCTION

Three specimens of a species resembling *Haustellotyphis cumingii* (Broderip, 1833) from the Pacific coast of Costa Rica were brought to my attention by Robert Koch of Phoenix, Arizona (Hertz, 1990). These specimens were collected dead at Bahía Tamarindo, Guanacaste Province, and Bahía Drake, Puntarenas Province, along with typical specimens of *H. cumingii*.

In 1993, it became apparent that there were two distinct species when Robert Koch collected 24 additional specimens of *Haustellotyphis* at Bahía Tamarindo. Twenty specimens, at least seven of which were collected alive, shared the characters of the species resembling *H. cumingii*. The other four specimens are typical *H. cumingii*. A search of the collections of the Santa Barbara Museum of Natural History, the San Diego Natural History Museum, and the Los Angeles County Museum of Natural History revealed no additional specimens of the new species.

Institutional abbreviations are as follows: AMNH, American Museum of Natural History; ANSP, Academy of Natural Sciences of Philadelphia; CAS, California

Academy of Sciences; LACM, Los Angeles County Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History; SDNHM, San Diego Natural History Museum; USNM, National Museum of Natural History, Smithsonian Institution.

SYSTEMATICS

TYPHIDAE Cossmann, 1903

Haustellotyphis Jousseaume, 1880

Type species: *Typhis cumingii* Broderip, 1833, by original designation.

Haustellotyphis wendita Hertz, sp. nov.

(Figures 1-4, 7, 9-10)

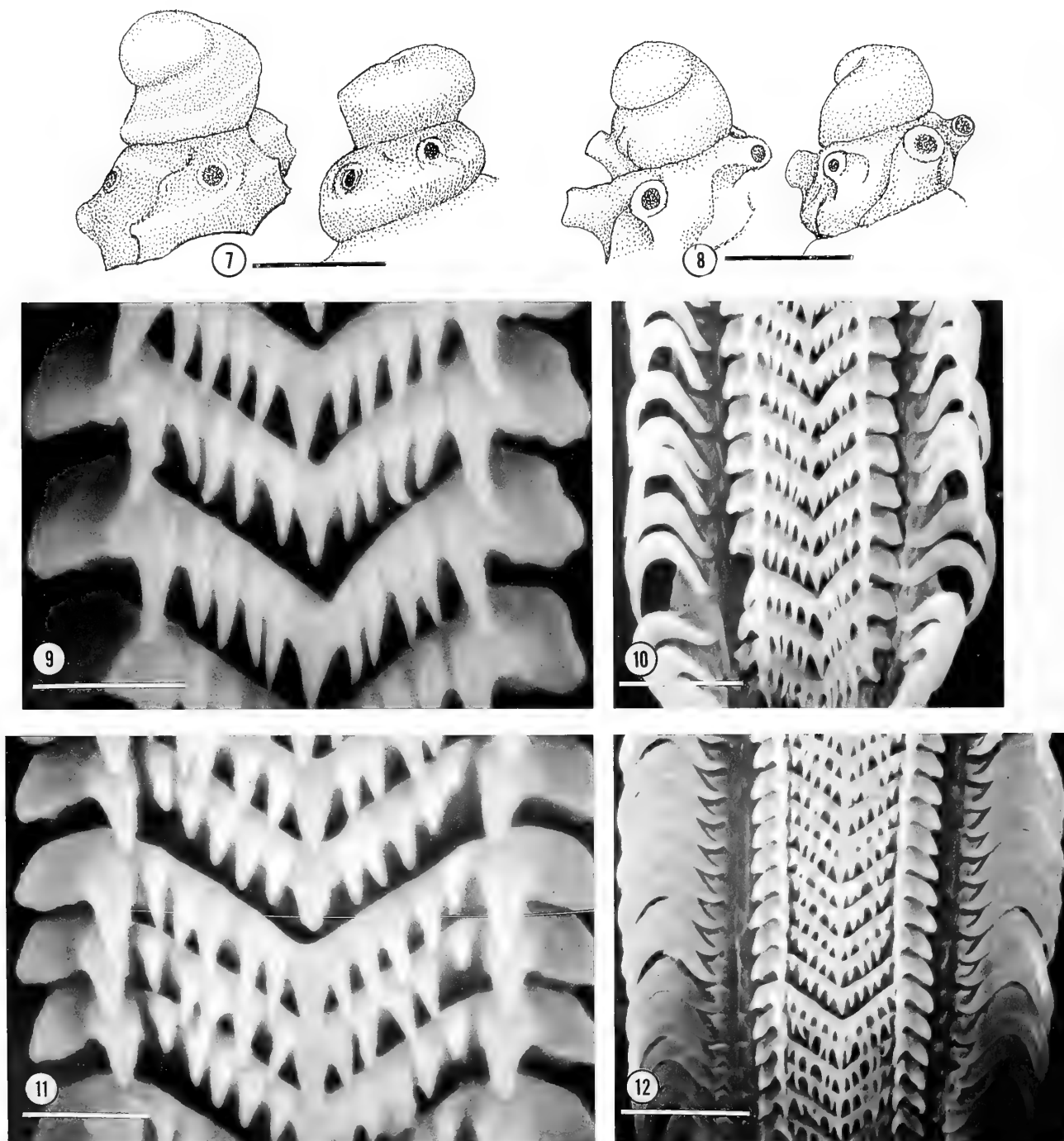
Description: Holotype 17.9 mm long, approximately 7 mm in diameter, excluding spines; protoconch of $2\frac{1}{4}$ smooth, off-white, angulate whorls, teleoconch of $4\frac{1}{2}$ whorls. Whorls with four varices; tubes beginning on first whorl of teleoconch on leading side of varical margin, three per whorl, tube openings round, area below tubes swollen. Shoulder well defined. Spines long where not broken, and flaring, apertural spine very long with partition. Siphonal canal long, straight, closed. Aperture entire, erect with projecting

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Figures 1-6

Figures 1, 2. *Haustellotyphis wendita* Hertz, sp. nov. Holotype SBMNH 142119. Length 17.9 mm, width approximately 7 mm. Figures 3, 4. *Haustellotyphis wendita* Hertz, sp. nov. Paratype AMNH 226509. Length 20.7 mm, width approximately 9 mm. Figures 5, 6. *Haustellotyphis cumingii*, 21.8 mm long, approximately 9 mm wide. S. of Santa Cruz, Nayarit, Mexico in 6-18 m in mud. December 1978. Leg. Carol & Paul Skoglund.





Figures 7-12

Figure 7. *Haustellotyphis wendita* Hertz, sp. nov. Two views of angulate protoconch. Scale bar = 500 μ m. Figure 8. *H. cumingii*. Two views of rounded protoconch. Scale bar = 480 μ m. Figures 9, 10. *H. wendita* Hertz, sp. nov. SEM photographs of radula of holotype, (9) closeup of three teeth. Scale bar = 10 μ m. (10) view of ribbon. Scale bar = 25 μ m. Figures 11, 12. *H. cumingii*. SEM photographs of radula of specimen photographed in Figures 5 & 6. (11) closeup of five teeth. Scale bar = 10 μ m. (12) view of ribbon. Scale bar = 34 μ m.

peristome. Varices on body whorl with three to five faint raised spiral threads fading out intervally; some intervarical areas completely lacking any hint of spiral threads; no nodes on varices. Apertural varix flaring, showing new growth, spiral cords on new growth somewhat raised and open, apertural spine closed. Radula with four denticles on either side of central cusp. Operculum corneous, leaf-shaped with concentric rings and terminal nucleus. Shell glossy brown with off-white to cream apertural spine and partition; protoconch and first teleoconch whorl glossy white.

Type locality: Off Playa Tamarindo, Bahía Tamarindo, Guanacaste Province (approx. 11°42'N, 85°50'W), dredged in 6–15 meters and Río Sierpe, Bahía Drake, Puntarenas Province (approx. 9°10'N, 83°40'W) dredged in 9–24 meters, both sites in Costa Rica.

Type material: Twenty-one specimens collected by Robert Koch on 6 & 8 March 1993 and 18 February 1988 from off Playa Tamarindo, Bahía Tamarindo, Guanacaste Province and two specimens from Río Sierpe, Bahía Drake, Puntarenas Province on 4 & 5 February 1979. Holotype: SBMNH 142119; Paratypes: 1 specimen SBMNH 142120; 2 specimens AMNH 226509; 2 specimens ANSP 398306; 2 specimens CASIZ 099054; 2 specimens LACM 2744; 2 specimens USNM 887134; 1 specimen, private collection of Carol Skoglund of Phoenix, Arizona; 1 specimen, private collection of the author (all from Tamarindo); 9 specimens Koch collection (7 from Tamarindo and 2 from Bahía Drake).

Distribution: *Haustellotyphis wendita* is known only from Playa Tamarindo, Bahía Tamarindo, Guanacaste Province, and Río Sierpe, Bahía Drake, Puntarenas Province, Costa Rica.

Discussion: Specimens of *H. wendita* studied ranged from juvenile specimens of less than 5 mm in length with two teleoconch whorls to mature specimens of five teleoconch whorls attaining a length of 22.8 mm. For comparison, nine specimens of *H. cumingii* from the Koch collection from Costa Rica and 19 specimens from the Skoglund collection from various localities in Mexico were examined (Figures 5, 6). These specimens have three to 5¾ teleoconch whorls and range in length from 6.0 to 22.6 mm. Several consistent differences were noted. All specimens of *H. cumingii* have a rounded protoconch of 1¾ whorls (Figure 8), whereas *H. wendita* has an angulate protoconch of 2¼ whorls (Figure 7). In specimens of *H. cumingii* (Figures 5, 6) the spines on the final whorl are posteriorly directed, whereas in *H. wendita* they flare out. The varices of *H. wendita* have faint raised spiral threads, whereas

the varical sculpture in *H. cumingii* is of strong, raised cords.

The central tooth of the radula of the holotype of *H. wendita* has five denticles on either side of its central cusp (Figures 9, 10), whereas the central tooth from a specimen of *H. cumingii* was found to have six denticles on either side of the central cusp (Figures 11, 12). However, Radwin & D'Attilio (1976:fig. 141) and Thiele (1931:fig. 318) show the radula of *H. cumingii* with four denticles on either side of the central tooth. As was shown in D'Attilio & Hertz (1988) there is considerable variation in radulae in the typhids, even on the ribbon of a single specimen in some species.

Specimens of *H. wendita* were found at two localities in Costa Rica approximately 300 km apart. At both locations *H. cumingii* was also found. *H. cumingii* also has a distribution from Acapulco, Oaxaca, Mexico, to Guayaquil, Ecuador (Keen, 1971), and north to Manzanillo, Colima, Mexico (Radwin & D'Attilio, 1976).

Etymology: It is with great pleasure that this new species is named in honor of Wendy Koch, who along with her husband, Robert, dredged the specimens of this new species.

ACKNOWLEDGMENTS

David K. Mulliner took the photographs of the specimens figured; Hugh Bradner took the SEM photographs, and Joyce Gemmell did the drawings of the protoconchs of the two species. My gratitude to them for their considerable help. Carol Skoglund generously lent comparative material from her collection, and James H. McLean and Emily H. Vokes kindly reviewed a draft of the manuscript and gave very helpful suggestions for which I thank them. Most of all I am indebted to Robert Koch for giving me the opportunity to describe this new species.

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The Biology and Functional Morphology of *Cooperella subdiaphana* (Carpenter) (Bivalvia: Petricolidae)

by

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Abstract. *Cooperella subdiaphana* Carpenter, 1864 from the west coast of North America is, on the basis of its anatomy, a member of the Petricolidae, allowing abandonment of the name Cooperellidae. It is possible that there are two species of *Cooperella* in California, one intertidal, the other subtidal. The lack of recent material prevents resolution of this question and, in the absence of any proof to the contrary, it is assumed that *C. subdiaphana* is a highly variable species, in terms of habitat, shell shape, and extent of fine ribbing.

Cooperella subdiaphana is of interest because under some as yet unknown conditions, it produces a secretion from pallial glands around the pedal gape which agglutinates surrounding sediments into a hard, oval block within which the bivalve is entombed. Access to the water column is via apertures for the separate siphons. Such a life style and structure is unique among the Bivalvia, the only comparison being with representatives of the Gastrochaenidae, and possibly derives from the ability of many petricolids, i.e., *Petricola* spp., to produce a pallial secretion which assists burrowing into soft rocks and shales.

Museum collections of *Cooperella subdiaphana* contain little recent material. This may result from the reclamation of Californian bays that has destroyed much of the habitat of this unusual bivalve.

INTRODUCTION

The Cooperellidae Dall, 1900, comprises a single genus, *Cooperella* Carpenter, 1864, with possibly four nominal species, all restricted to the east and west coasts of the Americas. The literature on the biology of one of these, *Cooperella subdiaphana* Carpenter, 1864, contains tantalizing references to an unusual life style. Abbott (1974: 536) stated that it "enwraps itself with agglutinated sand grains." Keen (1971:201) stated that "Specimens may be found intertidally in California constructing "nests" of agglutinated mud or sand in sheltered crevices." These statements derive from the observations of Keen & Frizzell (1939:23) who described the species as being covered in a "nest of agglutinated sand." Haas (1942) reported upon such specimens in the Los Angeles County Museum and in the collections of Stanford University. Haas (1943:12, fig. 7) published photographs of two nests from the Stanford collections, noting that the "dried covering is rather solid; it is closed all around, leaving only two slits on the

posterior extremity for the communication of the inmate with the outer world."

Although the number of species composing the genus *Cooperella* is not certain, neither is the taxonomic status of the family Cooperellidae. Early workers placed *Cooperella* in the Petricolidae Deshayes, 1839, e.g., Thiele (1935), although most subsequent and contemporary workers, e.g., Hertlein & Strong (1948), Olsson (1961), Keen (1971), Abbott (1974), and Boss (1982) placed it in the Cooperellidae. Most, however, place the family alongside the Petricolidae in the Veneroidea on the basis of the structure and arrangement of the hinge teeth.

Notwithstanding the above taxonomic studies, there is no other information on this enigmatic species, genus, and family. During the summer of 1993, I took the opportunity to visit California and inspect the Los Angeles County Museum and Stanford University material, the latter now held at the California Academy of Sciences, and to examine the large collection of dried material at the Santa Barbara Museum of Natural History.

The aims of this study were to investigate the anatomy of *Cooperella subdiaphana*, to explain how the species builds its remarkable "nest," and to ascertain the taxonomic status of the Cooperellidae.

MATERIALS AND METHODS

During July 1993, the collections of *Cooperella* in the Santa Barbara Museum of Natural History, comprising some thirty lots, were examined. The list of lots is not detailed here, but reference will be made in the text to specific ones. Also examined was material contained in the collections of the Natural History Museum, London (BMNH) (5 lots: Accession numbers, 2172, 1563a, b; 93.5.12.12.13, and no number). Material from the California Academy of Sciences (CAS) included three intact, preserved specimens. One specimen (Acc. No.: 077895) was dissected; one of two other specimens (Acc. No.: 19-0536), the largest (shell length 7.6 mm), was serially transversely sectioned, and alternative slides stained in Ehrlich's hematoxylin and eosin and Masson's trichrome. The third, smaller specimen of 4 mm shell length remains intact.

Material in the Los Angeles County Museum (LACM) contained one preserved specimen (LACM 59-94) of 7.5 mm shell length and was also left intact. The museum also had three dried individuals within their "nests" (LACM 150348). One of these was cut sagittally with a hacksaw to ascertain structure; the two other specimens were left intact. The above, with those in the collections at Stanford University (now at CAS) figured by Haas (1943), constitute the only specimens of *Cooperella subdiaphana* enclosed within nests. Similarly, the LACM 59-94 lot and the CAS 19-0536 specimen constitute the only known extant preserved material.

SYSTEMATICS

Palmer (1958) reviewed species described by P. P. Carpenter. These include *Oedalia subdiaphana* and *O. (Cooperella) scintillaeformis* (Carpenter, 1864:639). Palmer (1958) found that the holotype of *O. subdiaphana* in the collections of the United States National Museum (USNM No. 3563) was smashed while the syntypes of *O. scintillaeformis* USNM (No. 15669) comprise two intact specimens and a single valve.

Both *Oedalia (Cooperella) scintillaeformis* and *Oedalia subdiaphana* were validly described by Carpenter (1864). Dall (1900:1061-1065), as first reviser, selected *Cooperella* over *Oedalia* and *O. subdiaphana* over *O. scintillaeformis*; he also erected the family name Cooperellidae. This monogeneric family dates back to the upper Miocene (Yorktown) of Virginia and North Carolina and is represented today by *Cooperella atlantica* Rehder, 1943, found from southeast Florida to the Greater Antilles and Brazil (Abbott, 1974), *C. panamensis* Olsson, 1961, from Panama, and *C. subdiaphana*, found along the west coast of North

America, from British Columbia to near the head of the Gulf of California (Olsson, 1961).

A lot identified as *Cooperella panamensis* in the collections of the Santa Barbara Museum of Natural History (SBMNH No. 54167), from Playa Encantada, S.E. of Acapulco, Guerrero, Mexico, appears identical to the lots labelled *C. subdiaphana*, as does the illustration of the type of *C. panamensis* in Olsson (1961:pl. 84, fig. 5). It seems possible, therefore, that there are only two living species of *Cooperella*, i.e., *C. atlantica* on the east coast and *C. subdiaphana* on the west coast of North America, the ranges of both extending into South and Central America, respectively. It is, however, clear that Carpenter (1864) thought two species existed on the west coast, i.e., *C. scintillaeformis*, which he named but did not describe, and *C. subdiaphana*, the type of the genus. Subsequent authors, however, have followed Dall (1900) in synonymizing *C. scintillaeformis* with *C. subdiaphana*, e.g., Hertlein & Strong (1948), Palmer (1958), Olsson (1961), Keen (1971), and Abbott (1974). Palmer (1958) provides a list of synonymies.

Cooperella subdiaphana has a wide bathymetric range, occurring intertidally in numerous Californian bays, e.g., Newport Bay (SBMNH 08782), Anaheim Bay (SBMNH 19308 and 397; all collected alive), Mission Bay (SBMNH Jules Hertz Collection, no number; all collected alive), and from deeper waters offshore, e.g., 4-60 feet, La Jolla Canyon (SBMNH 24898), and from the stomach of an English sole, 20-25 fathoms, Santa Monica Bay (SBMNH 25157).

Some individuals in some lots, e.g., SBMNH 43538 and 44444M from deeper waters, are lightly radially ribbed, whereas intertidal individuals, e.g., SBMNH B. 3481, are not. One large lot (SBMNH 31584) from San Diego, comprising 14 intact shells and 29 valves, contains individuals which vary from elongate to squat, thicker to thinner, and lightly ribbed to unribbed. The data pertaining to all the lots is so variable, however, that it is not possible to divide specimens into separate taxa on the basis of shell form, degree of ribbing, and habitat. Much of the material is also beach-eroded, e.g., SBMNH 23413 (Goleta, California) and Jules Hertz collection (SBMNH, no number; 1979). From the material available, therefore, it is impossible to determine whether *Cooperella subdiaphana* is a single, highly variable, widely ranging (in terms of depth) species or is two variable species, one perhaps intertidal, the other subtidal. This question is unlikely to be resolved because individuals have not been collected alive for many years, e.g., CAS (077895; 1963), Jules Hertz Collection (SBMNH, no numbers; 1970, 1978, 1979).

The material investigated here is of a non-ribbed species, the intact specimens of which were all collected intertidally, e.g., CAS No. 077895; 19-0536, as were the "nests," e.g., LACM 150348. In the absence of any proof that two species occur in California, I refer to this species as *Cooperella subdiaphana* (Carpenter, 1864).

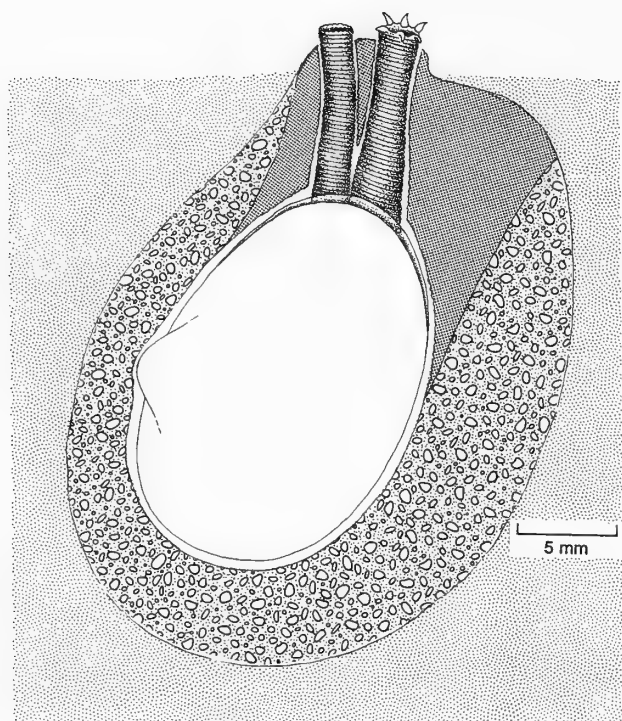


Figure 1

Cooperella subdiaphana inside its "castle," in turn embedded in sediment.

BIOLOGY

Cooperella subdiaphana occurs intertidally and subtidally, and the large number of lots in the collections of the Santa Barbara Museum of Natural History contain some which comprise numerous intact valves and were, therefore, living individuals, e.g., SBMNH 31521, 7 intact shells, 7 valves; SBMNH 397, 21 intact shells; SBMNH 31584, 14 intact shells, 29 valves; SBMNH 20627, 11 intact shells, 22 valves. The species could, therefore, once be collected easily, and there is no record that individual shells in the collections were removed from "nests." Some valves have been bored by naticids, e.g., SBMNH 31584, SBMNH 33526, and BMNH Acc. No. 2172. These valves were probably not bored while the animal lived inside a "nest," as naticids manipulate their prey in a stereotyped manner prior to boring (Ansell & Morton, 1985), and unlike muriciids, do not attack their prey aperturally without the need to hold their prey as, for example, do species of *Chicoreus* attacking boring lithophagine mytilids (Taylor, 1980). Only a few of the lots of *Cooperella subdiaphana* in the Santa Barbara Museum of Natural History contain information on life habitats. One (SBMNH 25157) was collected from the stomach of an English sole (*Parophrys retulus*) and another (CAS No. 077895) in the California Academy of Science collection was found under a board on a mud flat.

It is the specimens in "nests," however, that are of most

interest, i.e., SBMNH 20630; LACM 150348 (3 specimens). The "nest" does not comprise a mesh of byssal threads, as in many mytilids, e.g., *Musculista senhousia* (Benson, 1842) and *Arcuatula elegans* (Gray, 1828) (Morton, 1973, 1980), but is made of hard agglutinated sand and silt grains. It is so hard that a hacksaw blade was needed to cut it. Each specimen had, however, been dried for many years so it is possible that in life it was softer. The "nest" is approximately 30 mm long, oval, and somewhat laterally flattened with a slightly tapered posterior end. The tip of the posterior elongation has two small apertures which relate to the separate siphons. The anterior, antero-dorsal, ventral, and lateral parts of the "nest" are hard. Posteriorly, however, the "nest" is less solid and more crumbly in texture, although of definable form. The internal surface is smooth and accommodates the shell valves. Posteriorly, the internal surface is divided to form two narrow tubes, similarly smoothly lined, to accommodate the siphons. Photographs of the "nest" of *Cooperella subdiaphana* appear in Haas (1943:fig. 7). Figure 1 illustrates the encased animal in its postulated position in the sediment.

FUNCTIONAL MORPHOLOGY

The Shell

The shell of *Cooperella subdiaphana* is relatively small, the largest specimen examined being 17 mm in shell length from Crown Point, Mission Bay in the Jules Hertz collection (SBMNH; no number, 1978). The white shell is thin, brittle, and sometimes somewhat transparent. It is equivalve and ovately rectangular, some specimens being more elongate, others more squat (Figure 2A). The outer surface is smooth, with occasional concentric lines, and in some specimens, there is a light radial ribbing. The ovately rectangular shape seen in the shell is moderately inflated (Figure 2B), the umbones arching over the dorsal hinge line. Everywhere, the valve margins meet. The ligament is external and opisthodontic (Figures 2C & 3A, B). The shell in internal view (Figure 2D) shows that the pallial sinus (PS), extends far onto the anterior face of the shell.

The left valve (Figure 3A) has three small cardinal teeth, anterior (ACT), posterior (PCT), and central (CCT), the last of which is bifid. The right valve (Figure 3B) has two cardinals, anterior (ACT) and central (CCT), the last of which is also bifid.

The Organs of the Mantle Cavity

The adductor muscles (Figure 4, AA; PA) are small and isomyarian. Internal to each adductor is a small pedal retractor muscle (PPR). The ctenidia comprise two demibranchs of which the inner is large (ID), the outer small (OD). Only the anteriormost filaments of the inner demibranch extend between the labial palps (LP), those of the small outer demibranch terminating midway along the ctenidial axis. The ctenidial/labial palp junction is of Type

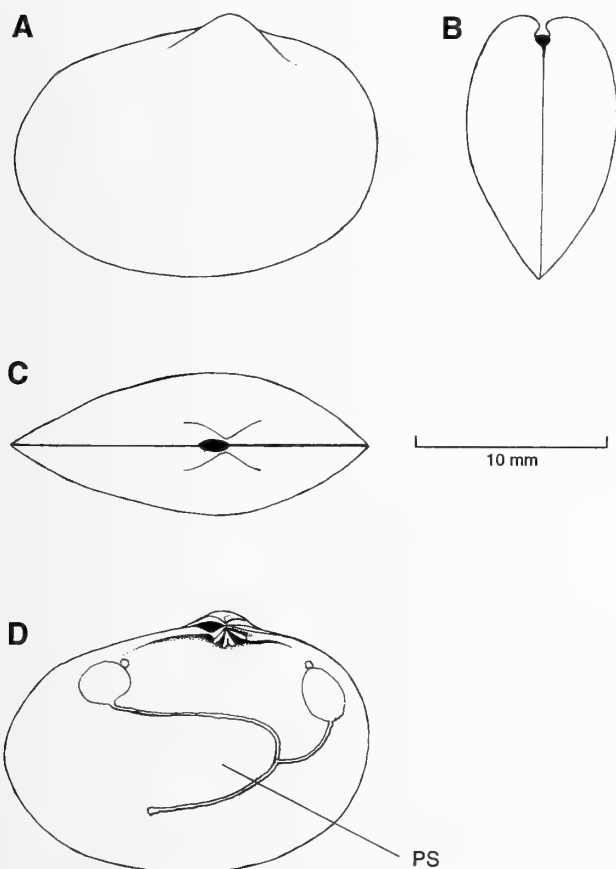


Figure 2

Cooperella subdiaphana. The shell as seen from A, the right side; B, the anterior; C, the dorsal aspects and D, an internal view of the left shell valve.

3 (Stasek, 1963), as found in *Claudiconcha japonica* Dunker, 1882 (Morton, 1978). There is a ventral marginal food groove on the inner demibranch only, so that the ciliary currents on the ctenidia probably conform to Type C(1) (Atkins, 1937), as found in *Petricola stellae* Narchi, 1975 and *Claudiconcha japonica* (Narchi, 1975; Morton, 1978). The labial palps (LP) are small, each with approximately 14 ridges. The visceral mass is large, the foot (F) small, with no byssus.

The Siphons

The siphons (Figure 4, ES; IS) are long and separate, the long siphonal retractor muscles (SRM) withdrawing them deeply between the shell valves. Each siphon is concentrically annulate. At their apices, the exhalant is lightly papillate, the inhalant bears six stubby tentacles.

The Mantle Margin

The mantle margin (Figure 4, MM) is extraordinarily thick around the pedal gape (PEG). Anterior and posterior

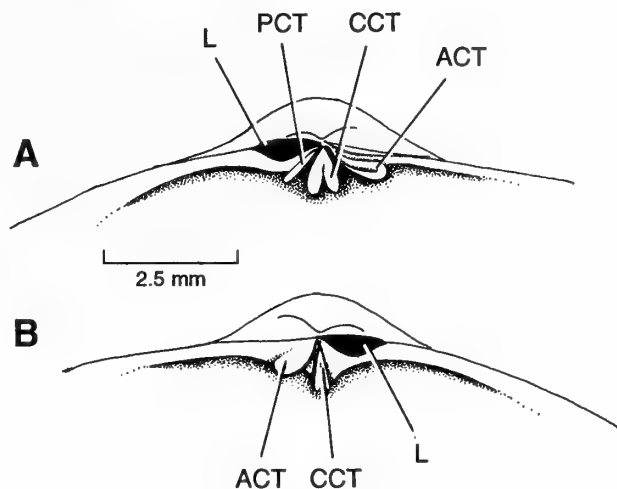


Figure 3

Cooperella subdiaphana. The hinge plate of A, the left and B, the right shell valves. Key: ACT, Anterior cardinal tooth; CCT, Central cardinal tooth; L, Ligament; PCT, Posterior cardinal tooth.

to the pedal gape, the mantle margins fuse (Figure 5). The mantle margin comprises three folds. The outer mantle fold (OMF) is small and secretes from its inner face a thin periostracum (P). The middle mantle fold is divided into two subfolds, an outer [MMF(2)] and an inner [MMF(1)]. The mantle margins fuse by means of the inner folds only (FIMF), i.e., type A (Yonge, 1982). There is a small pallial retractor muscle (PRM), a pallial nerve (PN), and the inner surface of the mantle is covered with cilia (C). Discharging onto the inner surface of the mantle are small (10–12 μ m) sub-epithelial basiphilic glands [PG (II)], which probably secrete mucus.

Around the pedal gape, the same arrangement of pallial folds can be seen (Figure 6). There is a ciliated rejectory tract (CRT) on the inner surface of the mantle, and the basiphilic subepithelial glands also occur [PG(II)]. The thickening of the mantle margin around the pedal gape is caused by a localized inflation of the haemocoel (HA) in conjunction with a large glandular area comprising elongate, eosinophilic, sub-epithelial cells discharging onto the inner surface of the mantle [PG(I)].

The Organs of the Visceral Mass

The visceral mass is large (Figure 7), the foot small (F). The pedal retractor muscles are also small (APR; PPR). In the visceral mass, the esophagus (OE) leads into a large stomach (S), with a separate crystalline style sac (CSS) opening into it from the postero-ventral wall. Anterior to this opens a slender midgut (MG) which progressively enlarges into a capacious hindgut (HG) packed with sediment and sand grains. This leads to a capacious rectum (R), also packed with sediment. The rectum penetrates

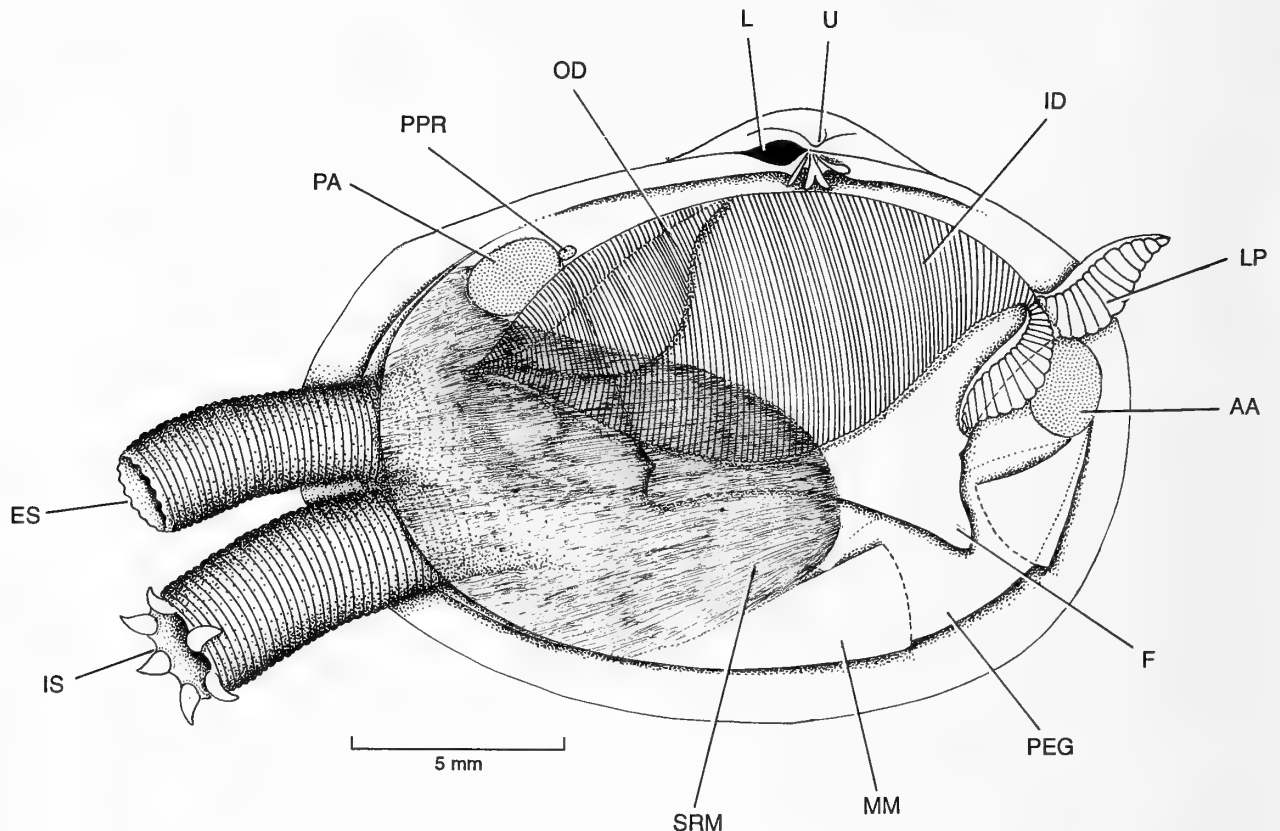


Figure 4

Cooperella subdiaphana. The organs of the mantle cavity as seen from the right side after removal of the right shell valve and most of the right mantle lobe. Key: AA, Anterior adductor muscle; ES, Exhalant siphon; F, Foot; ID, Inner demibranch; IS, Inhalant siphon; L, Ligament; LP, Labial palp; MM, Mantle margin; OD, Outer demibranch; PA, Posterior adductor muscle; PEG, Pedal gape; PPR, Posterior pedal retractor muscle; SRM, Siphonal retractor muscle.

the heart. The ventricle (V) is large with lateral auricles (A). The rectum then passes between the posterior pedal retractor muscles (PPR) over the posterior adductor muscle (PA) to end in an anus (A), which hangs freely from the posterior surface of the adductor. The paired kidneys (K) are located anterior to the posterior pedal retractor muscles. The sexes appear to be separate.

DISCUSSION

Cooperella was originally placed in the Petricolidae by Carpenter (1864) and though assigned to its own family by Dall (1900), the Cooperellidae has invariably been linked closely to the Petricolidae by subsequent authors.

There are a number of studies on the anatomy of representatives of the Petricolidae by Purchon (1955), Yonge (1958), Narchi (1974, 1975), Morton (1978), and Morton & Scott (1988). Petricolids are mostly rock borers, e.g., *Petricola carditoides* (Conrad, 1837) (Yonge, 1958), *P. pholadiformis* (Lamarck, 1818) (Purchon, 1955), and *P. lapicida* (Gmelin, 1791) (Morton & Scott, 1988). Originally

thought to be mechanical borers, e.g., *P. pholadiformis* (Purchon, 1955; Ansell & Nair, 1969), it is now believed that they are chemical borers. Morton & Scott (1988) identified large pallial glands around the pedal gape of *P. lapicida* that they believed produced the secretion facilitating this method of burrowing.

In the general features of its anatomy, but specifically with regard to the arrangement of hinge teeth, *Cooperella subdiaphana* is clearly a veneroid. The hinge teeth of many petricolids, e.g., *Petricola stellae* and *P. gracilis* Deshayes, 1853 (Narchi, 1975), *P. lapicida* (Morton & Scott, 1988), comprise three cardinals in the left valve, two in the right. Other authors, (Purchon, 1955; Morton, 1978) describe three teeth in the right valve of *Petricola pholadiformis* and *Claudiconcha japonica* Dunker, 1882, respectively, although both authors agree that personal interpretation of hinge teeth structure may account for such differences. As in other petricolids, e.g., *Petricola pholadiformis* (Purchon, 1955), *P. carditoides* (Yonge, 1958), *P. lapicida* (Morton & Scott, 1988), the siphons of *C. subdiaphana* are separate, and pallial fusion involves the inner folds only. As in all

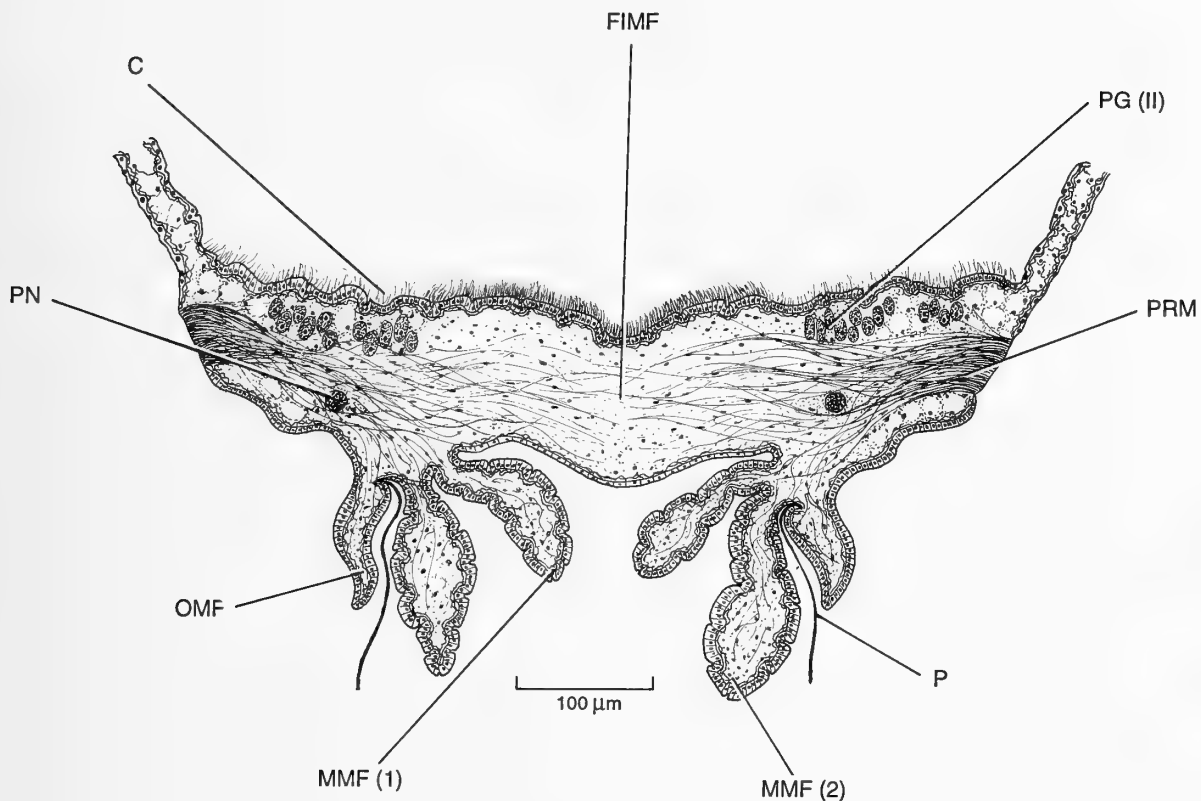


Figure 5

Cooperella subdiaphana. A transverse section through the fused mantle margins, posterior to the pedal gape. Key: C, Cilia; FIMF, Fused inner mantle folds; MMF(1), Inner component of the middle mantle fold; MMF(2), Outer component of the middle mantle fold; OMF, Outer mantle fold; P, Periostracum; PG(II), Pallial gland II; PN, Pallial nerve; PRM, Pallial retractor muscle.

petricolids, the ctenidial ciliation of *C. subdiaphana* is probably of type C(1) (Atkins, 1937), and the arrangement of the ctenidial-labial palp junction is of Type 3 (Stasek, 1963). Similarly, there is a poorly developed foot and no byssus, as in *P. carditoides* (Yonge, 1958). In the nestling *Claudiconcha japonica*, however, the foot is large and a byssus is present in the juvenile, but not the adult (Morton, 1978).

Cooperella subdiaphana is not a borer, but there are few records available to say how it does live. It has been collected by dredges, e.g., SBMNH 44444 M and SBMNH 43277, from subtidal depths, but it also occurs intertidally having, for example, been found under a piece of wood stranded on a mud flat (CAS No. 077895). The collections in the Santa Barbara Museum contain numerous lots which were collected alive, e.g., SBMNH 397 and SBMNH 20627. The species is bored by naticids, and one individual was recovered from the stomach of a flatfish. It is clear, therefore, that the life style of *C. subdiaphana* is variable, i.e., it can be a solitary nestler and occur more numerous as a burrower of intertidal and subtidal muds. The small size of its foot suggests, however, that *C. subdiaphana* must

be an inefficient burrower, possibly explaining why it was collected by dredges when one would expect, because of its long siphons and pallial sinus, that it would be buried deeply.

Some individuals of *Cooperella subdiaphana* are surrounded by agglutinated sand grains (Haas, 1943). It is clearly inappropriate to regard such a structure as a "nest" composed of woven fibers, as is typical of representatives of the Mytilidae, e.g., *Musculista senhousia* (Morton, 1973). It is also structurally different from the entombing tube of representatives of the Gastrochaenidae (Morton, 1985), e.g., *Eufistulana mumia* Spengler, 1783 (Morton, 1983). "Castle" might be a more appropriate term. The presently described "castles" are hard; it is unknown, however, if that of a living individual is softer. Such a life style is unusual, and I believe that the encapsulating "castle" is constructed by an outpouring of a secretion from the pallial glands around the pedal gape which binds the surrounding sediment, particularly anteriorly, laterally, antero-ventrally, and antero-dorsally. It is significant that the material of the "castle" is less agglutinated around the siphons. This is probably related to distance from the source

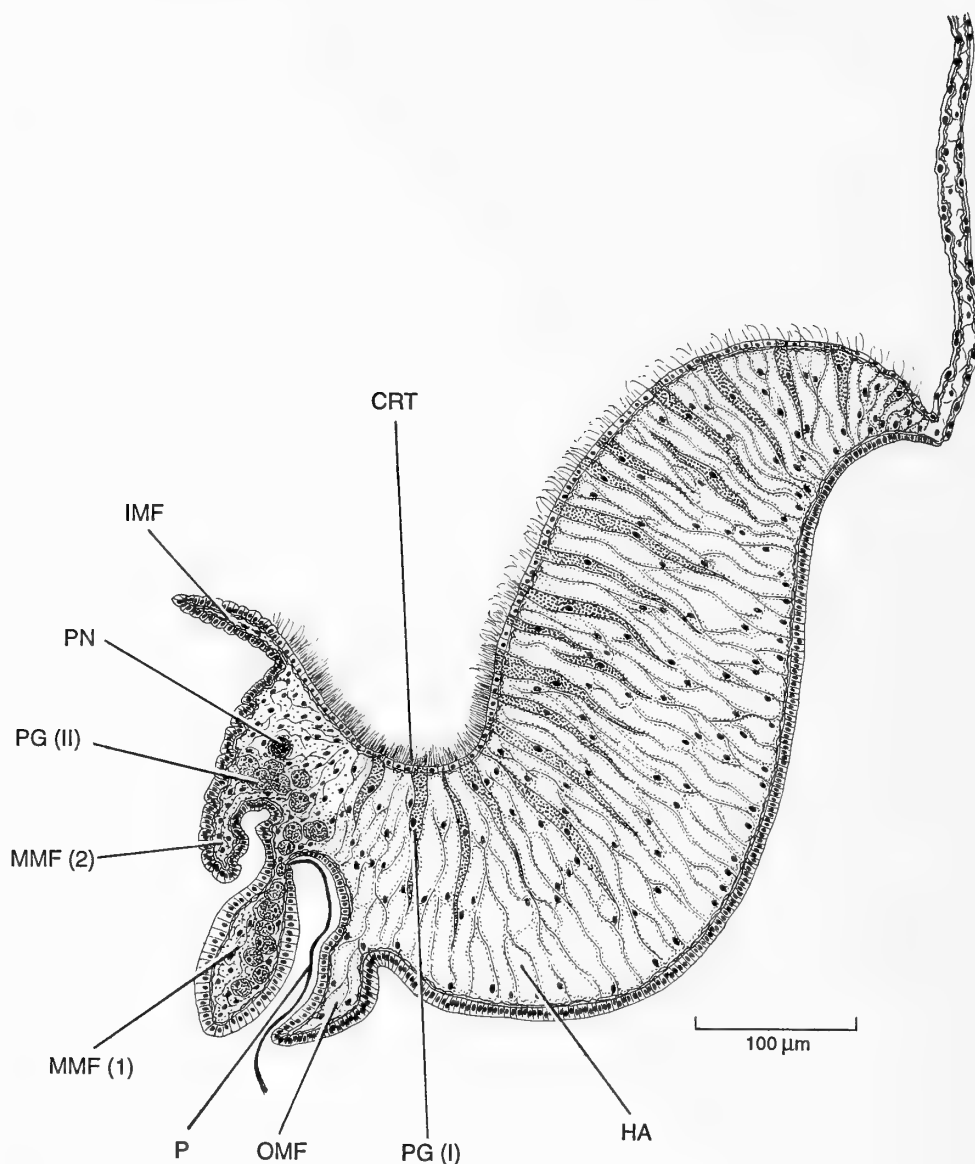


Figure 6

Cooperella subdiaphana. A transverse section through the right mantle lobe at the pedal gape. Key: CRT, Ciliary rejection tract; HA, Haemocoel; IMF, Inner mantle fold; MMF(1), Inner component of the middle mantle fold; MMF(2), Outer component of the middle mantle fold; OMF, Outer mantle fold; PG(I), Pallial gland I; PG(II), Pallial gland II.

of that secretion and the possible accumulation here of sediment, feces, and pseudofeces. The huge amounts of sediment in the gut of one of the dissected specimens indicates that the species is a deposit feeder, with the concomitant production of large quantities of feces and pseudofeces. The internal lining of the "castle" is smooth and approximates the contours of the shell so that other than the siphons, *Cooperella subdiaphana* does not move inside its home. It could not do so anyway because the siphons have to protrude posteriorly from the "castle" via well-defined apertures.

Cooperella subdiaphana can, therefore, in some circumstances, build a "castle", but normally does not. Perhaps only individuals that settle in an inhospitable habitat construct such structures.

Morton & Scott (1988) identified large glands around the pedal gape of *Petricola lapicida* believed to produce a secretion that facilitated chemical boring. Glands with a similar histology and distribution occur in *Cooperella subdiaphana*.

Morton (1978) suggested that the Petricolidae evolved as nestlers which subsequently adopted a chemical boring

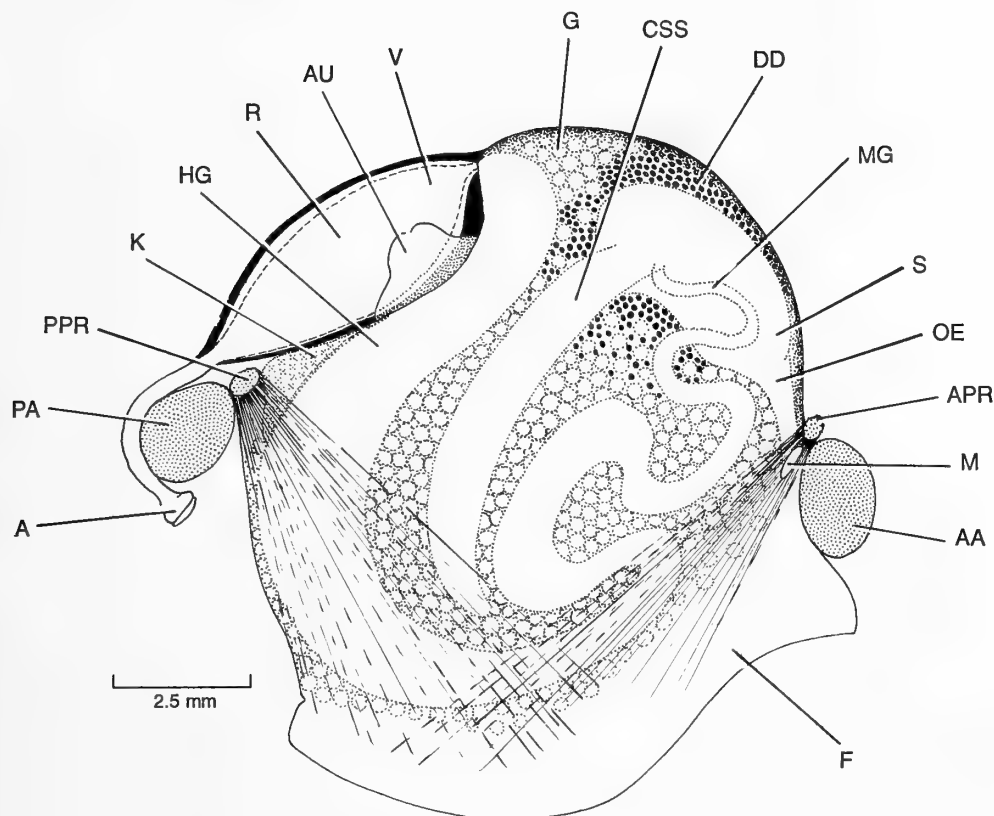


Figure 7

Cooperella subdiaphana. The organs of the visceral mass as seen from the right side. Key: A, Anus; AA, Anterior adductor muscle; APR, Anterior pedal retractor muscle; AU, auricle; CSS, Crystalline style sac; DD, Digestive diverticula; G, Gonad; HG, Hind gut; K, Kidney; M, Mouth; MG, Midgut; OE, Esophagus; PA, Posterior adductor muscle; PPR, Posterior pedal retractor muscle; R, Rectum; S, Stomach; V, Ventricle.

mode of life. *Cooperella subdiaphana* seems to have adopted a nestling, burrowing life style utilizing a secretion, not to chemically erode a burrow in soft rocks, but to agglutinate a "castle" within which it is entombed. Not all individuals do this, and it must be assumed that a "castle" is only produced under certain, as yet unknown circumstances. It is also probable that such entombed individuals cannot grow, so that the "castle" is possibly built when adult, by individuals that reside in inhospitable sediments or in response to a changing habitat such as burial.

Cooperella subdiaphana is a member of the Petricolidae, so that the family name Cooperellidae Dall, 1900 must be abandoned. It appears, however, that the Petricolidae are a more diverse family than hitherto appreciated. The family dates from the Caenozoic, possibly following the exploitation of inshore habitats by the Heterodonta after the post-Cretaceous mass extinction that left vacated marine habitats available for colonization by the radiating Veneroidea (Morton, 1990). Petricolids are mostly small, cryptic, and highly specialized nestlers (*Claudiconcha*), borers (*Petricola*), and now, "castle" builders in soft intertidal and subtidal sediments. Representatives of many bivalve phylogenies build "tubes," e.g., the Teredinidae,

Gastrochaenidae, and Clavagellidae (Morton, 1985) enabling immurement in sediments. The structure built by *Cooperella subdiaphana* is not, however, a "tube" of secreted calcium carbonate, but an agglutination of surrounding sediment bonded by a secretion that creates a virtually impregnable structure, the term for which is most appropriately "castle."

The collections of *Cooperella subdiaphana* contain virtually no material collected later than the 1970s. Much of the material comprises single separated valves collected offshore by dredges and bears no comparison with the large collections made in the earlier parts of this century. One has to wonder whether this species, with its remarkable, unique, highly specialized life style, has been endangered by the reclamation of bays that has occurred along much of the coast of California. The species is possibly endangered and is clearly deserving of a much more detailed investigation than this study of shells and cadavers.

ACKNOWLEDGMENTS

I am grateful to the director of the Santa Barbara Museum of Natural History for a travel grant enabling me to visit

California in 1993 and for permission to work on the collections. I am also grateful to Paul H. Scott for bringing together material from the Los Angeles County Museum, California Academy of Sciences, Stanford University, and his parent institution, the Santa Barbara Museum of Natural History, for me to work on. I am also grateful to Paul and his wife Kaylyn for much hospitality during my visit. The collections of the Natural History Museum, London, were also examined in the summer of 1993 through the courtesy of Dr. J. D. Taylor.

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The Recent Introduction of a Freshwater Asiatic Bivalve, *Limnoperna fortunei* (Mytilidae) into South America

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Abstract. The temporal and spatial distribution of *Limnoperna fortunei* in the Argentine littoral of the Río de la Plata is reported. Its distribution is limited by the most contaminated area and by an increment in the saline concentration. A decrease in density was recorded between August 1992 and January 1993. Subsequently there was an increase in density up to a maximum of 82,000 ind·m⁻² in May 1993. It is concluded that because of its functional and morphological characteristics, *L. fortunei* will spread quickly. With *Corbicula fluminea* and *C. largillierti*, *Limnoperna fortunei* is the third invading species to be introduced into South America from Southeast Asia. Its possible entry into Argentina, by trading ships from Korea and Hong Kong, is suggested. Import peaks correspond with the estimated arrival of these three invaders.

INTRODUCTION

Limnoperna fortunei (Dunker, 1857) (Mytilidae) is a freshwater species, which is found in rivers and streams of China and Southeast Asia (Morton, 1977). It was first discovered in South America in 1991, at Bagliardi (34°55'S–57°49'W) (Darrigran et al., 1993; Pastorino et al., 1993).

A great diversity of mollusks occurs along the littoral of the Río de la Plata, Argentina, and 27 species of gastropods and 23 species of bivalves have been recorded (Darrigran, 1991). There are six species of freshwater, infaunal bivalves, i.e., *Corbicula fluminea* (Müller, 1774), *C. largillierti* (Philippi, 1811), *Anodontites tenebrosus* (Lea, 1834), *Diplodon paranensis* (Lea, 1834), *Musculium argentinum* (d'Orbigny, 1835), and *Pisidium sterckianum* Pilsbry, 1897.

The only species of Mytilidae recorded from the Río de la Plata is *Mytella charruana* (d'Orbigny, 1842) (= *M. falcata* (d'Orbigny, 1842)), which occurs in Punta Piedras, Buenos Aires, Argentina (35°26'S–57°8'W) and in Montevideo, Uruguay (Darrigran, 1991).

The aim of the present work is to report upon the temporal and spatial distribution of *Limnoperna fortunei* (Dunker) in the littoral of the Río de la Plata, Argentina, and identify its way of arrival.

MATERIALS AND METHODS

Limnoperna fortunei populations occur on all available hard substrates such as trunks, roots, and stones, even on those placed artificially for coastal stabilization. In this case, they are found in the interstices formed by the piles of stones.

During summer 1993, samples were obtained from 10 littoral localities (Figure 1; Table 1). The discontinuous settlement of *L. fortunei* made the taking of samples difficult by uniform sampling protocol. Consequently, the area of the sampling quadrats varied according to the heterogeneity of the habitat. Taking into account such temporal variability, sampling was undertaken at approximately 60 day intervals in the locality where *L. fortunei* was first recorded from (Bagliardi).

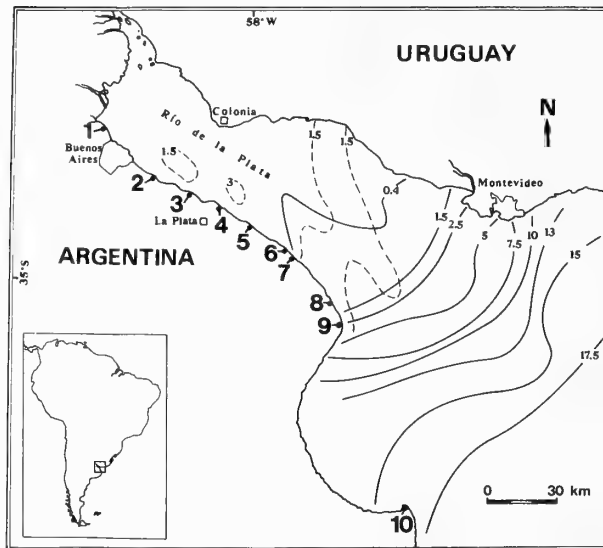


Figure 1

Map showing the sampling localities and isohalines along the Río de la Plata. Continuous lines correspond to average salinities during the 1982–1987 period; Broken lines correspond to an abnormal saline intrusion on 10 March 1984 (taken from Comisión Administradora del Río de la Plata, 1989). 1—Anchorena, 2—Quilmes, 3—Punta Lara, 4—Bagliardi, 5—Punta Blanca, 6—Atalaya, 7—Magdalena, 8—Punta Indio, 9—Punta Piedras, 10—Punta Rasa.

Values of average density were obtained using the following formula:

$$D = [\Sigma(n/a)/M]$$

where:

D: the average number of individuals $\cdot m^{-2}$

M: total number of samples

n: number of individuals sampled⁻¹

a: sampled area

To determine the possible introduction route, trade statistics between Argentina and the countries where this species is found, were analyzed. These values indirectly

express the number of ships that may have introduced it (Morton, 1987). Data were taken from the National Institute of Statistics and Census of the Argentine Republic (Instituto Nacional de Estadísticas y Censos—I.N.D.E.C., 1987–1991).

RESULTS

Description of the Environment

A marked temporal and spatial variability in salinity characterizes the Río de la Plata. Studies carried out on the littoral macrobenthos, showed that the Río de la Plata is freshwater from its origin up to an imaginary line linking Colonia (Uruguay) with La Plata (Argentina) (Darrigran, 1991). The remaining part is a large zone of poikilohaline waters whose temporal and spatial variation in salinity oscillates between 0.05‰ at the head to >25‰ at the river mouth.

The distribution of the littoral sedimentary facies shows a stepped arrangement of texture, being sandy at the river head and caliche at the mouth. Only in sampling localities 1 and 9 (Figure 1) was it possible to find caliche (natural hard substrata) or vegetation (sampling locality 5). Elsewhere, the scarce available hard substrata is anthropogenic (walls and piers).

The distribution pattern of *Limnoperna fortunei* is limited by a highly contaminated zone (localities 1 and 2) and by high salinities (localities 9 and 10). Table 2 shows several parameters of water quality. Sample localities 1 and 2 coincide with areas more polluted than the others, probably because of the proximity of factories and sewage of Buenos Aires City. Southward the pollution decreases and the salinity increases (see Table 2 and Figure 1). Low density at site 5 results from a lack of available hard substrata, since only roots and stems of *Scirpus californicus* (C. A. Mey) Steud, occur here (Figure 2).

Figure 3 shows the temporal variation in *Limnoperna fortunei* densities at Bagliardi. It was first found here, in September 1991, as isolated groups of five or six individuals. In May 1992, the average density was 31,222 individuals $\cdot m^{-2}$; a decrease was then observed from August

Table 1

Sample localities on the coast of the Río de la Plata (n = number of samples).

Sample localities		Date	n	Substrata
1. Anchorena	34°29'S–58°28'W	03/93	–	caliche
2. Quilmes	34°45'S–58°13'W	02/93	–	stones
3. Punta Lara	34°48'S–57°59'W	01/93	3	stones
4. Bagliardi	34°55'S–57°49'W	02/93	3	stones
5. Punta Blanca	34°56'S–57°40'W	05/93	2	sand/roots
6. Atalaya	35°00'S–57°33'W	01/93	2	stones
7. Magdalena	35°01'S–57°31'W	01/93	2	stones
8. Punta Indio	35°15'S–57°14'W	03/93	2	stones
9. Punta Piedras	35°26'S–57°08'W	03/93	3	caliche
10. Punta Rasa	35°46'S–56°50'W	03/93	–	caliche/stones

Table 2

Parameters of water quality (taken from A.G.O.S.B.A, O.S.N., S.I.H.N., 1992). DO = dissolved oxygen, mg $O_2 \cdot L^{-1}$; BDO = biological oxygen demand, mg $O_2 \cdot L^{-1}$; COD = chemical oxygen demand, mg $O_2 \cdot L^{-1}$; C = chlorides, mg $\cdot L^{-1}$; S = sulfates, mg $\cdot L^{-1}$; SM = suspension material, mg $\cdot L^{-1}$; T = turbidity, NTU; Na, Pb, K, mg $\cdot L^{-1}$; As, $\mu g \cdot L^{-1}$

Localities	Parameters										
	DO	BDO	COD	C	S	SM	T	Na	Pb	As	K
San Isidro 34°28'S-58°28'W	3.4	1.3	14.2	16	18	145	28	15.8	6	6.4	2.6
Palermo 34°34'S-58°25'W	3.2	3.5	4.2	19	15	87.9	50	19.8	18	6.4	3.7
Riachuelo 34°38'S-58°21'W	0.0	3.9	16.9	46	—	27.6	49	46.7	10	10.4	4.2
Santo Domingo 34°39'S-58°18'W	2.5	3.3	22.0	29	22	70.8	24	32.5	13	7.5	32.5
Bernal 34°43'S-58°19'W	4.5	10.4	17.0	48	—	43.4	—	52.3	15	10.4	4.2
Berazategui 34°45'S-58°11'W	3.1	11.1	30.0	40	27	2.4	28	41.9	8	9.6	3.8
Punta Colorada 34°46'S-58°08'W	0.2	11.6	30.0	36	20	35.8	35	37.8	13	8.6	4.2
Punta Lara 34°48'S-57°59'W	1.7	0.5	30.0	32	22	37.0	28	33.7	16	7.5	3.7
Water pumping 34°49'S-57°55'W	4.7	5.3	11.7	31	20	35.4	39	31.6	3	6.8	3.7
Sewage, Spill-Out 34°52'S-57°49'W	4.7	4.1	21.7	27	20	80.4	37	27.7	15	6.4	3.3

1992 to January 1993. Average density increased from February 1993 onward. The decrease in density recorded in March 1993 could be explained by a flooding of the Paraná River, the most important tributary of the Río de la Plata. In May 1993, it was 82,151 individuals $\cdot m^{-2}$, more than twice the numbers reported upon a year before.

DISCUSSION

Limnoperna fortunei is the third freshwater bivalve invading species which has used the Río de la Plata to enter South America. Ituarte (1981) reported the first occurrence in the Río de la Plata of two bivalve species from Southeast Asia: *Corbicula fluminea* (Müller, 1774) and *C. largillierti* (Philippi, 1844). Adaptive and reproductive characteristics allowed *C. fluminea* to expand rapidly in the Río de la

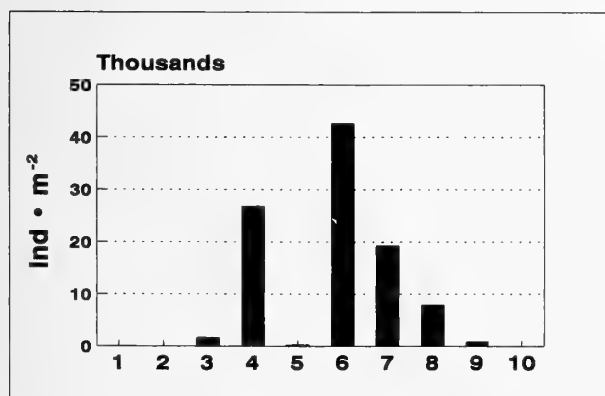


Figure 2

Average density of *Limnoperna fortunei* at each sampling locality (see Table 1). 1—Anchorena, 2—Quilmes, 3—Punta Lara, 4—Bagliardi, 5—Punta Blanca, 6—Atalaya, 7—Magdalena, 8—Punta Indio, 9—Punta Piedras, 10—Punta Rasa. Ind = individuals.

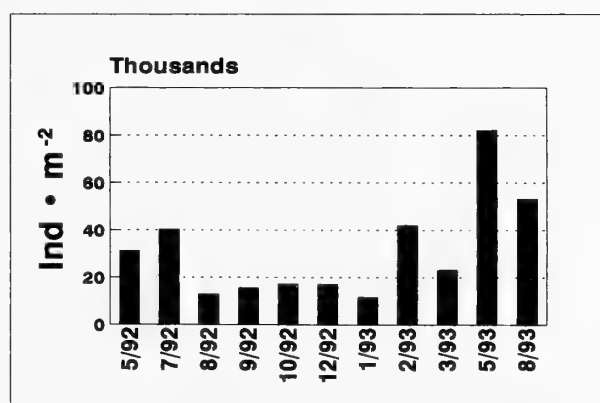


Figure 3

Average density of *Limnoperna fortunei* at the sampling locality at Bagliardi from May 1992 to September 1993. Ind = individuals.

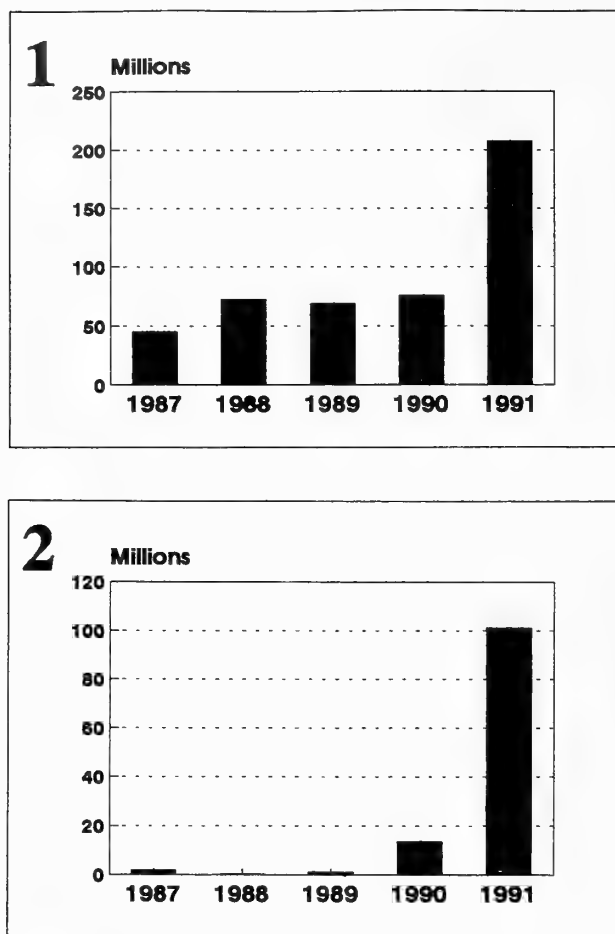


Figure 4

Argentine imports from Korea (1) and Hong Kong (2) from 1987 to 1991 in United States dollars (taken from I.N.D.E.C., 1987–91).

Plata estuary (Darrigran 1992), but also in the rivers Paraná and Uruguay. Corigliano & Malpassi (1993) have reported upon the presence of the genus *Corbicula* in the central part of Argentina (32°30'S–62°30'W), illustrating its potential for continuous expansion.

Trade by those countries where these invading species live, is carried out by ship. Allen (1953), Carlton (1992), and recently Carlton & Geller (1993) have argued for stricter controls of vessels departing such countries with a view to limiting the chances of introductions.

Ituarte (1981) suggests that *Corbicula* was introduced to Argentina between 1965 and 1975. Argentinian imports from Southeast Asian countries during that period were increased. In addition, this species is used as food in Asia; it may have been introduced alive for crew consumption.

A similar analysis may be done regarding *Limnoperna fortunei*. Continuous sampling in the Río de la Plata supports the suggestion that this species was introduced in

1991. Figure 4 shows the increase in Argentinian imports from Hong Kong and Korea. As the country with the steepest increment in imports is Hong Kong (more than fivefold times) and the presence of *Limnoperna fortunei* is confirmed (Morton, 1987), it seems to be the source of the Argentinian population of this species. Although it is not used as food, it may have been transported in tanks containing untreated fresh water.

Morton (1973) reported that *Limnoperna fortunei* has morpho-functional characteristics which would allow its rapid introduction elsewhere, as with *Corbicula fluminea* (Müller) in the United States and *Dreissena polymorpha* (Pallas, 1771) in Europe and North America (Hunter & Bailey, 1992).

Limnoperna fortunei has become ecologically and economically important because of the following factors: (1) Its epibyssate habit has no competition in the Río de la Plata littoral. (2) This species has a high biotic potential. Its invasion involves biofouling processes, affecting potable water supply systems for either human consumption or industrial use.

A stricter biological control of overseas ships is argued for.

ACKNOWLEDGMENTS

We wish to acknowledge Professor B. Morton for kindly helping us to identify *Limnoperna fortunei*, and C. Solari Yrigoyen who provided us with valuable information about Argentinian imports. We are grateful to C. Sutton and M. Griffin for help with the English version of this manuscript. Thoughtful reviews were provided by Dr. R. T. Dillon and an anonymous reviewer. Financial support was provided by the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina.

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The Gastropod *Philine bisculptata* Hanna,
1927, from the Eocene of Southern California,
Belongs in the Neritid Genus
Otostoma d'Archiac, 1859

by

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Abstract. Examination of new specimens of the gastropod *Philine bisculptata* Hanna, 1927, a rare fossil in the "Domengine Stage" (upper lower to lower middle Eocene) and "Transition Stage" (middle Eocene) of the San Diego area of southern California, reveals that the species belongs to the neritid genus *Otostoma* d'Archiac, 1859. *Otostoma bisculptata* is reported for the first time from the "Capay Stage" (middle lower Eocene) Maniobra Formation in the northern Orocochia Mountains, Riverside County, southern California. *Otostoma* is a Tethyan genus that ranges from Cretaceous to Eocene, with most species of Cretaceous age, and *Otostoma bisculptata* is the first confirmed Eocene report of this genus.

INTRODUCTION

Hanna (1927), in his monographic study of Eocene mega-invertebrate faunas from the San Diego area, assigned one of his new species, *Philine bisculptata* Hanna (1927:330, pl. 57, figs. 4, 7), to the opisthobranch genus *Philine* Ascanius, 1772. Hanna's illustrations of the holotype, which is a cast (consolidated sediment that filled a natural mold and produced a replica of the shell), are the only published illustrations of this rather rare species. It is impossible to discern the shape of the aperture of this species from Hanna's illustrations because the aperture is embedded in rock matrix. Recently, while examining Eocene megafossils in the collection of the Natural History Museum of Los Angeles County, I came across several specimens of Hanna's species. All of these specimens are casts, and, in a few cases, the apertures were exposed or could be cleaned of rock matrix. I also borrowed specimens of Hanna's species from other museums in southern California, and all of these specimens are also casts. Small patches of shell are present on a few specimens. Based on the new specimens, and especially those whose apertures are observable, it was possible to determine that Hanna's species actually belongs to the neritid *Otostoma* d'Archiac, 1859, a genus known

primarily from Cretaceous rocks in the Old World Tethyan paleobiogeographic province.

The molluscan stages used in this report stem from Clark & Vokes (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos," "Capay," "Domengine," "Transition," and "Tejon," from oldest to youngest. The stage names are in quotes because they are informal terms. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein.

Abbreviations used are: CAS, California Academy of Sciences, San Francisco; CSUN, California State University, Northridge; LACM, Natural History Museum of Los Angeles County, Malacology Section; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section; SDNHM, San Diego Natural History Museum; UCR, University of California, Riverside.

STRATIGRAPHY

Hanna (1927) gave only a general location for the type locality (CAS loc. 826) of *Philine bisculptata* and mentioned that it is in Rose Canyon, which is about 3 km southeast of La Jolla in the northern part of the metropolitan area

of San Diego (Figure 1). He assigned the strata at the type locality to the Rose Canyon shale member of the La Jolla Formation of Hanna (1926). Kennedy & Moore (1971) reassigned this formation to their Mount Soledad Formation, Ardath Shale, Scripps Formation, and Friars Formation, but only the Ardath Shale and Scripps Formations crop out in Rose Canyon (Kennedy, 1975). The stratigraphic position of the type locality of *P. bisculptata*, therefore, must be within the Ardath Shale or Scripps Formation. Both of these formations have been assigned by Givens & Kennedy (1979) to the "Domengine Stage" (upper lower to lower middle Eocene) and to the "Transition" "Stage" (middle Eocene).

Recently, seven additional specimens of *Otostoma bisculptata* were found in the LACMIP collection of Eocene mollusks from the San Diego area. Most of these specimens had been purchased from part of a collection made in the early 1900s by Charles H. Sternberg, but detailed locality information is not known. The scant information available on most of the old labels indicates Ardath Shale in Rose Canyon and Tecolote Canyon as the source areas (Figure 1). One of these old localities in Rose Canyon is equivalent to LACMIP loc. 26. A few of the specimens, however, were collected by workers other than Sternberg from LACMIP loc. 7193 in the Ardath Shale on Soledad Mountain just west of Rose Canyon. Another specimen was found in SDNHM collection (SDNHM loc. 1667) from the Ardath Shale in the Rose Canyon area. The Ardath Shale may represent a multitude of depositional environments ranging from submarine canyon fill to a tidal- or wave-dominated shelf (Link & Abbott, 1991).

Givens & Kennedy (1979:88, table 3) reported *Philine bisculptata* from five localities in the San Diego area. One locality (UCR loc. 4944) is from east of Rose Canyon, and the other four (UCR locs. 4975, 4982, 4987, 4990) are from Tecolote Canyon (Figure 1). They assigned all of these localities to the middle Eocene ("Transition Stage") upper part of the Scripps Formation. The Scripps Formation crosses paleoenvironmental boundaries, and some parts represent submarine-canyon fill, whereas other parts represent shelf deposits (May & Warme, 1991).

A few years ago, I collected a specimen of *Otostoma bisculptata* from the "Capay Stage" (middle lower Eocene) Maniobra Formation in the northern Orocopia Mountains, Riverside County, southern California (Figure 1). The specimen, which is a crushed cast, was collected at CSUN loc. 662 near the base of the formation. This locality was originally discovered by Crowell and Susuki (1959) and referred to as locality "F." The locality is in a thin, sandy mudstone lens containing abundant mollusks and other invertebrates. The mollusks lived in normal salinity at shallow depths adjacent to a submarine canyon and were transported a short distance basinward into the bathyal depths of a slope environment (Squires & Advocate, 1986; Advocate et al., 1988; Squires, 1991). Several of the mollusks from CSUN loc. 662 show very close affinities with Old World Tethyan species (Squires & Advocate, 1986).



Figure 1

Geographic distribution of *Otostoma bisculptata* (Hanna, 1927). Locality areas numbered from north to south. (1) Northern Orocopia Mountains, Riverside County; (2) San Clemente Canyon, San Diego County; (3) Soledad Mountain, San Diego County; (4) Rose Canyon, San Diego County; (5) Tecolote Canyon, San Diego County.

SYSTEMATIC PALEONTOLOGY

Family NERITIDAE Rafinesque, 1815

Subfamily NERITINAE Rafinesque, 1815

Genus *Otostoma* d'Archiac, 1859

Type species: *Nerita rugosa* Hoeninghaus, 1830, by indication Douvillé, 1904; see Squires & Saul (1993) for a thorough discussion of the complex history of the type species of *Otostoma*.

Otostoma bisculptata (Hanna, 1927)

(Figures 2–6)

Philine bisculptata Hanna, 1927:330, pl. 57, figs. 4, 7; Givens & Kennedy, 1979:88, table 3.

Supplementary description: Shell thin, medium-sized. Spire very low, apex depressed below flattened and smooth posteriormost surface of body whorl. Body whorl neritiform and enlarging moderately rapidly with a subangulate shoulder in parietal area and a rounded shoulder elsewhere. Body whorl with a prominent spiral ridge on medial part of whorl, and numerous and closely spaced axial ribs that weaken greatly anterior to the prominent spiral ridge. Adjacent axial ribs can coalesce. Posteriormost part of body whorl with one or two very weak spiral ribs that parallel the edge of the columella in the parietal region of the aperture. Columella concave and smooth and delineated by a slight raised area. Aperture elongate but with a continuous peristome.



Explanation of Figures 2 to 6

Figures 2-6. *Otostoma bisculptata* (Hanna, 1927). Figures 2-3: holotype CAS 2189, $\times 2.1$. Figure 2: abapertural view. Figure 3: side view. Figures 4-6: hypotype LACMIP 12353. Figure 4: apertural view, $\times 2.4$. Figure 5: abapertural view, $\times 2.3$. Figure 6: dorsal view, $\times 2.4$.

Type material and type locality: Holotype CAS 2189, Ardath Shale or Scripps Formation, Rose Canyon, San Diego.

Geographic distribution: Northern Orocochia Mountains, Riverside County, and San Diego, San Diego County, southern California.

Stratigraphic distribution: "Capay Stage" (middle lower Eocene), "Domengine Stage" (upper lower to lower middle Eocene), and "Transition Stage" (middle Eocene). "CAPAY STAGE": Lower Maniobra Formation, northern Orocochia Mountains, Riverside County, southern California (herein). "DOMENGINE STAGE" to "TRANSITION STAGE": Ardath Shale, San Diego County, southern California (herein); upper Scripps Formation, San Diego County, southern California (Givens & Kennedy, 1979).

Remarks: A total of 14 specimens were examined for this study. All are casts and replicate the external morphology quite well. The largest specimen (height 16 mm, width 22 mm) is the holotype (Figures 2-3). The specimen that shows the aperture the best is hypotype LACMIP 12353 (Figures 4-6).

Davies (1971) noted that *Philine* has an evolute body whorl that is very loosely coiled with an extremely wide aperture. A study of two LACMNH specimens of the extant *Philine alba* Mattox, 1958, found living at depths of 140 m off the coast of Los Angeles, underscored how

remarkably wide the aperture is in *Philine*. *Otostoma bisculptata* is clearly different from any species of *Philine* because *O. bisculptata* has a body whorl that is neritiform rather than loosely coiled, an aperture with a continuous peristome, an aperture that is narrower and smaller, and a body whorl with strong axial sculpture rather than smooth or with spiral striae. The globose shell with low spire and strong axial rib that characterizes *O. bisculptata* indicates assignment to the neritid *Otostoma*. Normally, *Otostoma* has a columella with strong teeth but the inner lip is especially prone to postmortem dissolution. *Otostoma* was originally characterized as lacking a neritid columella (d'Archiac, 1859) because the available specimens had undergone selective dissolution (Squires & Saul, 1993). Dissolution similarly affected the thin-shelled *O. bisculptata*.

Otostoma bisculptata has a very close affinity to *Otostoma tchihatcheffi* d'Archiac (1859:873-874, pl. 19, figs. 1a-c) and to *O. ponticum* d'Archiac (1859:874-875, pl. 19, figs. 2, 2a, 3), both from the Cretaceous of Asia Minor. *Otostoma bisculptata* differs from both by having a spiral rib on the medial part of the body whorl. In addition, *O. bisculptata* differs from *O. ponticum* by having weaker axial ribbing on the anterior part of the body whorl and having no tendency to develop cancellate sculpture in that region.

Wenz (1938) and Davies (1971) reported the geologic range of *Otostoma* to be Cretaceous to Paleocene and its distribution to be cosmopolitan. *Otostoma bisculptata* represents the first confirmed report of an Eocene species of genus *Otostoma*. Glibert (1962) reported *O. equinus* (Be-

zancon, 1870:320–321, pl. 10, fig. 5) from the lower and middle Eocene (Ypresian and Lutetian Stages) of the Paris Basin, France, but, as reported by Squires & Saul (1993), more work is needed to determine if "*O.*" *equinus* belongs in *Otostoma* or in the closely related genus *Velates* Montfort, 1810. *Otostoma bisculptata* differs significantly from "*O.*" *equinus* in having the following features: larger shell, a single spiral rib rather than four or five, more numerous and more closely spaced axial ribs, axial ribs unnoded, and axial ribs nearly obsolete rather than prominent on the anterior half of body whorl.

Otostoma is a Tethyan genus and most species are from the Old World. Previously, the only report of *Otostoma* from the Pacific coast of North America was that of Squires & Saul (1993), who reported a single specimen of *Otostoma aethes* Squires & Saul (1993:261–263, figs. 2–4) from uppermost Cretaceous or possibly lowermost Paleocene strata on the south side of Lake Nacimiento, San Luis Obispo County, California. *Otostoma bisculptata* differs from *O. aethes* in having the following features: smaller shell, apex of spire slightly depressed rather than slightly elevated, numerous closely spaced axial ribs on the body whorl shoulder, and a prominent spiral rib on medial part of body whorl rather than several low and noded spiral ribs on anterior third of body whorl.

ACKNOWLEDGMENTS

James H. McLean (Natural History Museum of Los Angeles County, Malacology Section) helped greatly with the proper identification of this species. Edward C. Wilson (Natural History Museum of Los Angeles County, Invertebrate Paleontology Section) allowed access to the collections and provided locality information. Jean DeMouthe (California Academy of Sciences, San Francisco), Tom Deméré (San Diego Natural History Museum), and Marilyn Kooser (University of California, Riverside) loaned specimens. Lindsey T. Groves (Natural History Museum of Los Angeles County) helped in finding additional specimens of Hanna's species in the LACMIP collections and loaned Recent material. The manuscript benefited from the comments of two anonymous reviewers.

LOCALITIES CITED

Unless otherwise noted, all localities are in strata of late early Eocene to middle Eocene age (equivalent to "Domengine" to "Transition" "Stages") and on the U.S. Geological Survey, 7.5-minute, La Jolla Quadrangle, 1967, San Diego County, San Diego.

CAS 826. Rose Canyon near San Diego, southern California (Hanna, 1927:265). Ardath Shale or Scripps Formation. Collector: R. A. Coleman, about 1915.

CSUN 662. At 2190 ft. elevation along the crest of a small hill, 137 m south and 31 m west of the NE corner of section 25, T. 6 S, R. 12 E, U.S. Geological Survey, 7.5-minute, Canyon Spring NW Quadrangle, 1963,

northern Orocopia Mountains, Riverside County, southern California. Lower Maniobra Formation. Age: Middle early Eocene ("Capay Stage"). Collector: R. L. Squires, 1992. [Locality is equivalent to loc. F of Crowell & Susuki, 1959].

LACMIP 26. Rose Canyon, San Diego County, California. Ardath Shale. Collector: C. H. Sternberg.

LACMIP 7193. 7700 ft. S71°E from triangulation point on Soledad Mountain. Ardath Shale. Collector: D. W. Scharf, 1930.

SDNHM 1667. Rose Canyon, San Diego County, California. Ardath Shale.

UCR 4944. At elevation of 80 m in terraced road cut on W side of Regents Road where it enters San Clemente Canyon from the south, 33,350 m N, 79,880 m E in zone 11 of the UTM grid system. Scripps Formation, approximately 30 m stratigraphically above base (Givens & Kennedy, 1979:93).

UCR 4975. At elevation of 60 m on N side of fourth eastern tributary to Tecolote Canyon, S of the E fork of the canyon, 27,155 m N, 83,050 m E in zone 11 of the UTM grid system. Scripps Formation, about 5 m stratigraphically below top (Givens & Kennedy, 1979:93).

UCR 4982. At elevation of 50 m in same tributary canyon as UCR loc. 4975, 27,070 m N, 83,110 m E in zone 11 of the UTM grid system. Scripps Formation, about 10 m stratigraphically below top (Givens & Kennedy, 1979:93).

UCR 4987. At elevation of 50 m on W wall of Tecolote Canyon, 26,575 m N, 82,545 m E in zone 11 of the UTM grid system. Scripps Formation, upper part (Givens & Kennedy, 1979:93).

UCR 4990. At elevation of 25 m in artificial excavation on N wall of Mission Valley, 25 m N of Friars Road and 25,335 m N, 82,590 m E in zone 11 of the UTM grid system. Scripps Formation, approximately 25 m stratigraphically below top (Givens & Kennedy, 1979:93).

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NOTES, INFORMATION & NEWS

Announcement of Computerization of a Large Land Snail Collection

The Field Museum's Division of Invertebrates recently completed an NSF-funded project to rehouse and computerize over 40,000 lots of Eastern North American terrestrial mollusks collected by Leslie Hubricht over a 60 year period from the 1920s to the 1980s. Long series of nearly every terrestrial mollusk species from this area are represented, including paratypes of many of Mr. Hubricht's species. Information requests and loans are available to the research community. Inquiries should be addressed to: John Slapcinsky, Division of Invertebrates, The Field Museum, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605, U.S.A., phone: (312) 922-9410.

Anterior Breakage and Repair in Two Species of the Gastropod Genus *Conus* (Gastropoda: Conidae)

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Introduction

Repaired scars left on body whorl of shells of *Conus* Linnaeus, 1758, indicating a roughly parallel damage of an earlier outer lip, or a large hole on the dorsum of the shell, have already been reported and interpreted as unsuccessful crab attacks (Currey & Kohn, 1976; Zipser & Vermeij, 1980; Vermeij, 1987, 1989; Kohn, 1992a). Repair after breakage of the anterior third of the shell is reported here for the first time. Vermeij (1987, 1989) emphasized that we critically need data on the likelihood of encounters between these gastropods and their enemies; therefore the frequency of repair of the anterior third of the shell is surveyed and compared with frequency of repair of the outer lip reported in the literature.

A specimen of *Conus marylandicus* Green, 1830, of the Tertiary period had its shell seriously injured, probably due to a crab attack. Post-scar shell growth seen on the shell surface demonstrates that the gastropod managed to escape an attempt at predation. A similar pattern of scar and shell repair found in a Recent specimen of *Conus regularis* Sowerby, 1833, indicates that two distinct species must have exhibited a similar protective behavior during different geologic periods. As far as it is known, *C. marylandicus* occurs only in Pliocene strata of eastern North America (Olsson & Harbison, 1953; Kohn, 1992b), and

became extinct sometime beyond the Pleistocene, when significant changes in oceanographic conditions (Keigwin, 1982) affected the molluscan faunas of the Caribbean and north-western Atlantic region (Vermeij, 1989; Allmon, 1992). While *C. regularis* is a constituent of the Recent fauna of western America (Hanna, 1963; Kohn, 1992b), it is also found in lower Pliocene strata of Carmen Island, Gulf of California (Hanna, 1963).

The protective behavior of withdrawing into the shell (Currey & Kohn, 1976; Vermeij, 1989; Kohn, 1992a) to survive predator attacks is reconstructed with details in this study, and is inferred from the form of shell damage. I have seen four shells with broken-away anteriors, two of which have been repaired. The repair frequency of the anterior third of the shell in *Conus marylandicus* and *C. regularis* is lower than the repair frequencies of the outer lip in several species of *Conus*. Therefore, the inferred behavior in response to the pattern of shell breakage reported herein appears to be rare or at least rarely successful.

Materials and Methods

I examined more than 10,000 shells of several species of *Conus*, from the Miocene to the Recent, in the following museums: Museu Oceanográfico de Rio Grande, Museum d'Histoire naturelle de Genève, Zoologisch Museum—Universiteit Van Amsterdam, Institut Royal des Sciences Naturelles de Belgique, Florida Museum of Natural History, California Academy of Sciences, Museum of Paleontology—University of California Berkeley (UCMP), and in my own collection (FHAC).

Repair frequencies of the anterior third of the shell were estimated by dividing the number of scars on the last whorl by the number of shells, following Currey & Kohn (1976), Zipser & Vermeij (1980), Vermeij (1987, 1989), and Kohn (1992a). These frequencies were based on 18 shells in UCMP and on four shells in FHAC of *Conus marylandicus* from Florida; and on 106 shells in UCMP of *C. regularis* from the eastern Pacific (Table 1).

Results

One fossil of *Conus marylandicus* (Figures 1–3) from Pliocene strata of the Caloosahatchee Formation, Saint Petersburg, Pinellas County, Florida, has a deep scar located in the left side of the last whorl, about 150° back from the outer lip and roughly parallel to it (Figures 2, 3). The scar runs from the suture to a point beyond the anterior third of the shell, indicating that peeling off of the outer lip took place during the attack. The scar then turns abruptly, and runs transversely to the shell axis, deep into the aperture (Figures 1, 2), indicating that the anterior

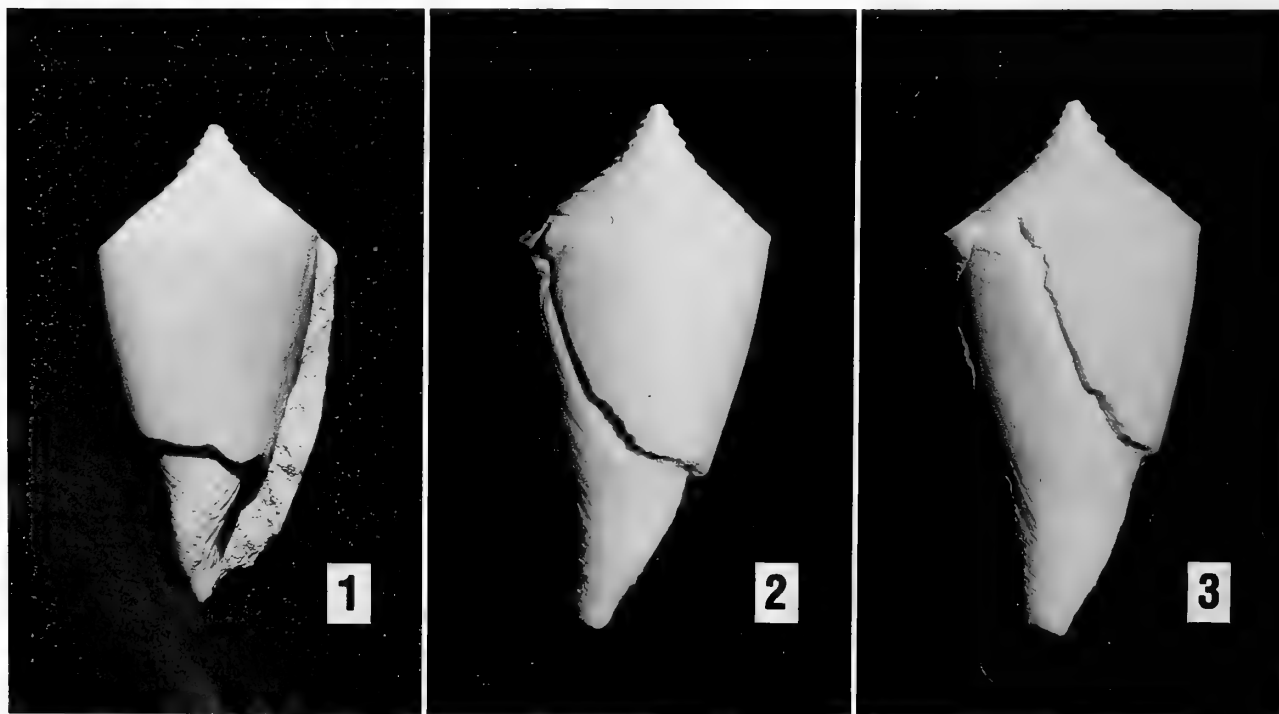
Table 1

Repair frequencies of anterior third (AT) and outer lip (OL) in shells of *Conus*. EP, Eastern Pacific; IP, Indo-Pacific; R, site of repair; S-N, number of samples (*s*) or number of individuals (*n*) (when available); WA, Western Atlantic.

R	F	S-N	Species	Region and age	Source
OL	1.2	<i>n</i> = 39	<i>C. lividus</i>	Hawaii, Recent	Currey & Kohn (1976)
OL	0.27	—	<i>C. sponsalis</i>	Guam, Recent	Zipser & Vermeij (1980)
OL	0.11	<i>s</i> = 8	3 species	Europe, Eocene	Vermeij (1987)
OL	0.29	<i>s</i> = 16	9 species	Europe, Miocene	Vermeij (1987)
OL	0.39	<i>s</i> = 21	4 species	WA, Recent	Vermeij (1989)
OL	0.29	<i>s</i> = 59	14 species	IP, Recent	Vermeij (1989)
OL	0.18	<i>s</i> = 15	7 species	EP, Recent	Vermeij (1989)
OL	0.06	<i>n</i> = 107	<i>C. striatus</i>	IP, Recent	Kohn (1992a)
OL	0.8	<i>n</i> = 29	<i>C. striatus</i>	IP, Recent	Vermeij (in litt.) (Kohn, 1992a)
AT	0.04	<i>n</i> = 22	<i>C. marylandicus</i>	Florida, Pliocene	This study
AT	0.009	<i>n</i> = 106	<i>C. regularis</i>	EP, Recent	This study

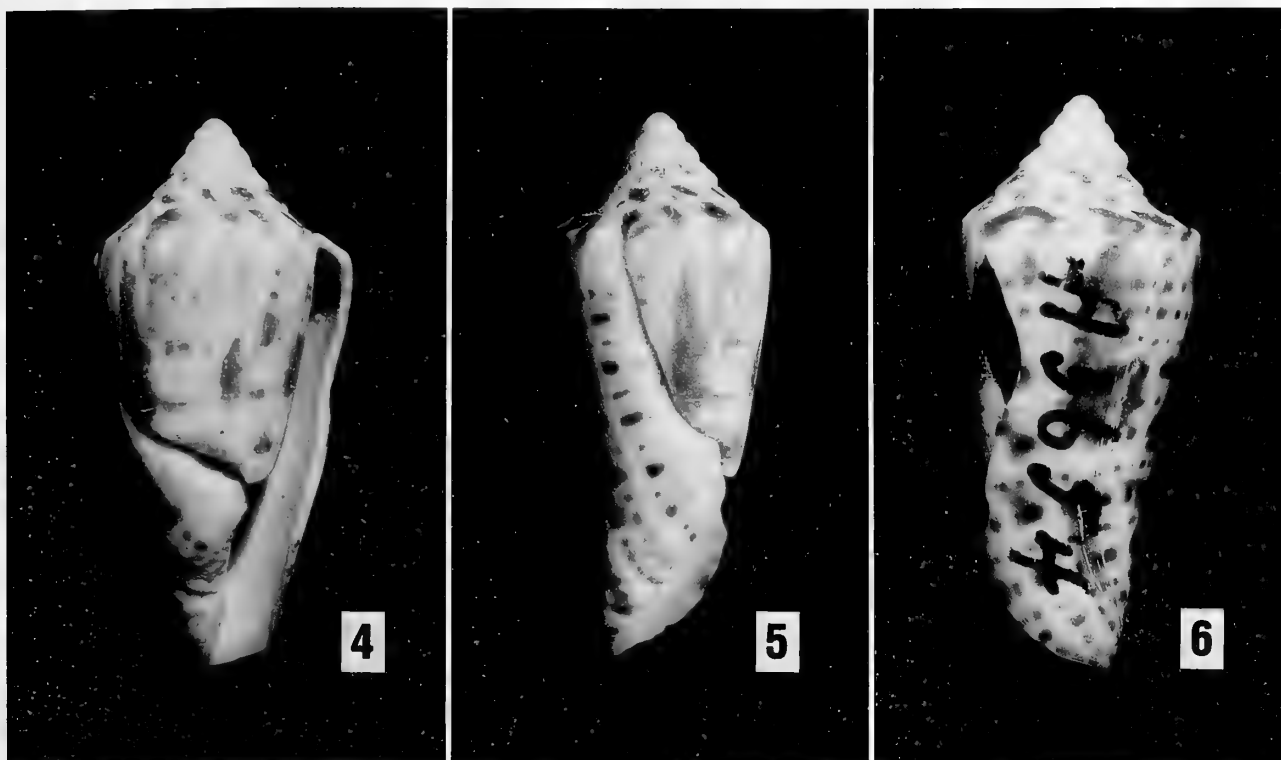
third of the shell was also broken away. Another scar, shallow and jagged, located on the dorsal side of the body whorl, about 90° back from the outer lip and parallel to it, indicates that the shell suffered a second episode of damage. Shell growth after the scars is characterized by the normal pattern of axial and spiral shell sculpture and inconspicuous spiral color rows. A siphonal canal slightly bent upward, not normal in the genus *Conus*, is conspicuously developed after the scar (Figure 2).

One shell of *Conus regularis* (Figures 4–6) from the Recent fauna of Angel de la Guarda Island, Gulf of California, Mexico, shows similar patterns of scarring and shell repair. A deep scar, located about 180° back from the outer lip and relatively parallel to it, runs from the suture to a point beyond the anterior third of the shell, where it turns into the direction of and deep into the aperture (Figures 4, 5), indicating peeling off of the earlier outer lip and crushing off of the anterior third of the shell. The



Figures 1–3

Conus marylandicus Green, 1830. Caloosahatchee Formation, St. Petersburg, Pinellas County, Florida, length = 25.6 mm, maximum width = 12.7 mm (FHAC). 1. Ventral side, showing the anterior transverse part of the scar. 2. Left side, showing the axial and beginning of the transverse scar, and the siphonal canal bent upward. 3. Dorsal side, showing the axial part of the scar.



Figures 4–6

Conus regularis Sowerby, 1833. Angel de la Guarda Island, Gulf of California, length = 26.0 mm, maximum width = 11.9 mm (UCMP A3654). 4. Ventral side, showing the anterior transverse part of the scar. 5. Left side, showing the axial and beginning of the transverse scar, the normal color pattern after the scar, and the siphonal canal bent upward. 6. Right side, showing the normal color pattern in the last half whorl, and the siphonal canal bent upward.

broken spiral rows of brown square spots and irregular axial flammules, characteristic of the species, are deposited in shell material after the scar (Figures 5, 6), and shell sculpture such as basal spiral striae remains in the last half whorl. An anomalous siphonal canal slightly bent upward was also developed after the scar in this specimen (Figures 5, 6).

Repair frequencies of the anterior third of the shell in *Conus marylandicus* of 0.04 ($n = 22$) and in *C. regularis* of 0.009 ($n = 106$), are conspicuously low when compared with repair frequencies of the outer lip surveyed for other species of *Conus* (Table 1).

Discussion and Conclusions

Although identifying exactly the unsuccessful predator of marine gastropods on the basis of scars left on their shells may be a subject open for discussion, I agree with Currey & Kohn (1976), Vermeij (1987, 1989), and Kohn (1992a) that such scars are strong evidence of past encounters with predatory crustaceans. The behavior of withdrawing into the shell to avoid crab attacks pointed out by Currey & Kohn (1976), Vermeij (1989), and Kohn (1992a), seems to have occurred in two distinct steps in both *Conus marylandicus* and in *C. regularis*. In the first step, during the

peeling off of the outer lip, the gastropods spirally retracted the whole body within their shells; in the second step, when the anterior third of the shell was broken away, both species managed to axially retract their foreparts, including siphon, head, and anterior part of the foot (Figure 7).

It could be speculated that these gastropods could have survived the attack by simply spirally retracting the whole body within the shell to a point beyond the anterior breakage, but there is some evidence that the inferred behavior of axially retracting the soft foreparts avoided decapitation that would otherwise have been lethal to *Conus marylandicus* and *C. regularis*. Several species of *Conus* that I have examined (Costa, 1988, 1990, 1994), withdrew spirally into their shells when disturbed but kept their foot, head, and siphon visible within the aperture, thus leaving the soft foreparts vulnerable to an eventual anterior shell breakage, unless axial retraction of the foreparts takes place (Figure 7). The three species of the *Conus jaspideus* Gmelin, 1791, complex of the western Atlantic (Costa, 1994) reacted positively when I touched their foreparts with a sharp object (pencil point); they axially withdrew the siphon and head, but kept the foot visible within the aperture. Vermeij (1978) illustrated a shell of *Conus flavidus* Lamarck, 1810, which had its anteriormost part crushed during a lethal xantid crab attack in the laboratory

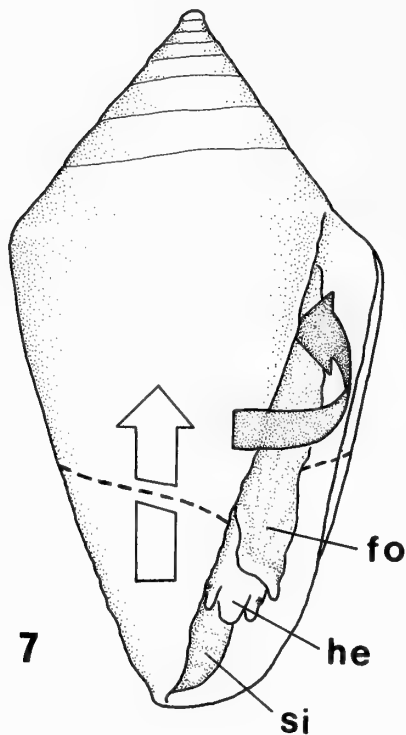


Figure 7

Diagram of the protective behavior of a *Conus* within its shell, showing the body spiral retraction (dark arrow), the site of anterior shell crushing (dashed lines), and the inferred axial retraction of the foreparts (light arrow). Key: fo, foot; he, head; si, siphon.

at Guam. In addition I have observed two empty shells with similar signs of trauma, one of *Conus sponsalis* Hwass in Bruguière, 1792, from Fiji, Pacific Ocean, and the other of *Conus clerii* Reeve, 1843, from off Cabo Frio, Rio de Janeiro, Brazil, the former in the collection of UCMP, and the latter in FHAC. These two shells have had their anterior third broken away with no sign of repair or growth after shell breakage, which indicates successful attacks and vulnerability of the soft foreparts.

Kohn (1992a) noted that changes in color pattern are frequent in shell material secreted after repair of broken outer lips, in unsuccessful attacks on *Conus*. This may be explained by stress to the mantle edge, which has a peripheral band that secretes the outer shell layer (Wilbur & Saleuddin, 1983). Since no changes in the pattern of pigment deposition in the outer shell layer occurred in *Conus marylandicus* or in *C. regularis*, the normal color pattern after shell repair indicates that the mantle edge was not affected during the attacks.

Repair frequencies of the anterior third of the shell in *Conus marylandicus* of 0.04 and in *C. regularis* of 0.009, are conspicuously lower than the repair frequency of the outer lip surveyed by Kohn (1992a) for *Conus striatus*

Linnaeus, 1758 (Table 1). This author stressed that the average number of 0.06 repairs per last whorl in *C. striatus* is lower than in most other species surveyed.

Although Vermeij (1978) pointed out that morphological adaptations rather than behavioral adaptations are expected from gastropods against rapidly moving attackers, these two cases studied herein involving distinct *Conus* species seem to contrapose the expectations.

Acknowledgments

I wish to express my gratitude to Drs. David R. Lindberg and Carole S. Hickman, for providing research facilities at the Museum of Paleontology, University of California Berkeley; to Drs. Alan J. Kohn and Geerat J. Vermeij for supplying literature; to Drs. Barry Roth and Geerat J. Vermeij for valuable comments.

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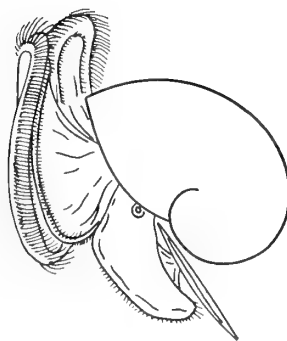
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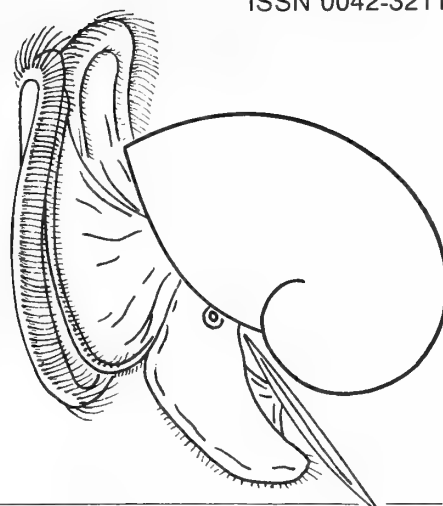
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THE VELIGER

A Quarterly published by
CALIFORNIA MALACOOZOOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor



Volume 38

July 3, 1995

Number 3

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The Veliger (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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Artificial Fertilization and Development through Hatching in the Oceanic Squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* (Cephalopoda: Ommastrephidae)

by

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Abstract. A technique for routinely obtaining hatchlings of oceanic squids via artificial fertilization is not available at present. This paper makes a major advance in that direction. A technique for artificial fertilization and rearing the resulting embryos through hatching for the oceanic ommastrephid squids *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* is presented that emphasizes the importance of egg hydration and methods of obtaining chorion expansion. Initial results comparing hatching time against rearing temperature show an expected decrease in time with increasing temperature.

INTRODUCTION

Experimental embryologists have artificially fertilized loliginid eggs for many years, but rearing the resulting embryos through hatching has been infrequent (Klein & Jaffe, 1984). Artificial fertilization of oceanic squids was first accomplished in *Todarodes pacificus* (Steenstrup, 1880) (Soeda, 1952, 1954) and has been repeated a number of times since (e.g., Hayashi, 1960). Except for the preliminary work of Arnold & O'Dor (1990) and the results of Sakurai & Ikeda (1994), artificially fertilized oceanic squid eggs have not been reared through hatching. In most cases, embryonic development stopped in the early developmental stages. For those embryos that survived the initial stages, death resulted from either failure of the chorion to expand, which constricted the embryo, or from bacterial infection.

Klein & Jaffe (1984) cultured fertilized embryos of *Loligo pealei* LeSueur, 1821 through hatching in petri dishes lined with agarose. Arnold & O'Dor (1990) provided more details concerning the Klein & Jaffe study: embryos were placed in depressions in the agarose; only partial lifting of the chorion occurred and only some embryos

hatched. They concluded "the stimulus to chorionic swelling is, in part, due to general factors associated with being enclosed in a jelly-like substance rather than a specific factor in the egg jelly derived from the nidamental gland" (Arnold & O'Dor, 1990:22). Ikeda & Shimizaki (in press) have found, however, that nidamental gland jelly will not cause chorion expansion in *Todarodes pacificus*.

Arnold & O'Dor (1990) added lyophilized nidamental gland material to the water surrounding the eggs of *Sthenoteuthis oualaniensis* (Lesson, 1830) and *Abraliopsis* sp. to facilitate raising of the chorion. They did not mention, however, whether or not the chorion actually lifted in their embryos. Their photographs show that it did not lift in *Sthenoteuthis* and only partially lifted in *Abraliopsis*. Since *Abraliopsis* lacks nidamental glands, the partial lifting of the chorion in this species suggests that the presence of a gel alone may, in some species, be important in obtaining chorion expansion.

Ikeda et al. (1993b) surrounded embryos of the ommastrephid squid, *Todarodes pacificus*, with lyophilized oviducal gland. Their selection of the oviducal gland was based on the likelihood that jelly from this gland, rather

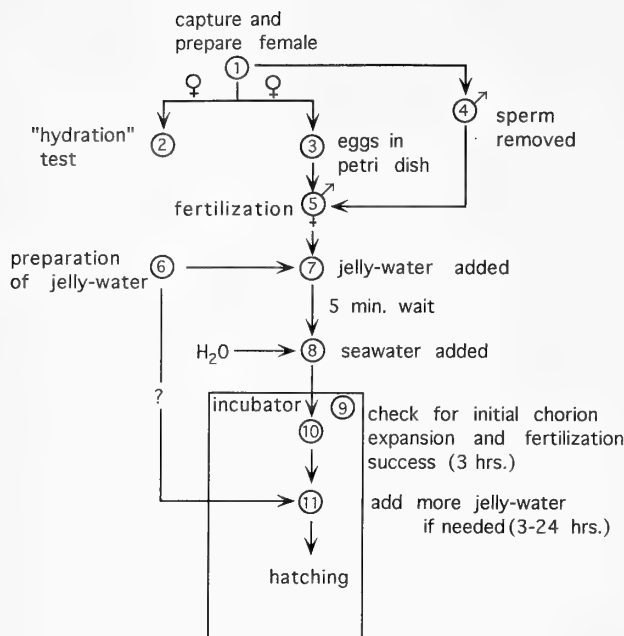


Figure 1

Schematic presentation of the protocol developed for artificial fertilization and rearing of embryos.

than the nidamental gland, first coats the eggs during spawning as suggested by Hamabe, 1962. They demonstrated that the initial phase of chorion expansion occurred only when the oviducal jelly was present. This approach, along with some innovations in general technique, enabled Sakurai & Ikeda (1994) to successfully hatch artificially fertilized eggs of this species.

Here we report on attempts to apply this latter technique, with modification, to two additional species of oceanic squids, the ommastrephids *Sthenoteuthis oualaniensis* and *Ommastrephes bartramii* (LeSueur, 1821). Our interest in hatching embryos of artificially fertilized oceanic squids is directed toward problems of maintaining, feeding, and rearing paralarval oceanic squids. Our present inability to study living paralarvae in the laboratory severely limits our knowledge of the biology of these early life stages. The first step in solving these problems is to obtain a large and consistent supply of hatchlings. At present, rearing artificially fertilized embryos seems the only feasible approach to this problem.

MATERIALS AND METHODS

Attempts at artificial fertilization were made during five cruises near Hawaii between 1992 and 1994. Three were with the FTS *Hokusei Maru* from Hokkaido University, one with the R/V *Moana Wave* from the University of Hawaii, and one with the R/V *Wecoma* from Oregon State

University. Artificial fertilization experiments, always a second priority on these cruises, were limited by time and available resources.

To determine percent of successful fertilization, 20 eggs in each of two orthogonal transects across each dish containing eggs and sperm were evaluated for cleavage. These counts are conservative since some fertilized eggs were not recognized as having cleaved due to their orientation.

The most critical step in rearing squid embryos is to obtain chorion expansion. Chorion expansion occurs primarily in two stages. The first occurs 30 to 60 min (24°C) after fertilization and is a very distinct enlargement of the perivitelline space (e.g., see photographs in Ikeda et al., 1993a). The second occurs around 48 hr (24°C) after fertilization when the embryo begins to elongate. The second enlargement can occur even when the first enlargement did not, although the total expansion will be less than normal (Figure 5A, B). In such cases, however, hatching can still occur. When chorion expansion failed entirely, the increasingly compressed embryos continued to develop for up to 72 hr, but death followed as the embryo began to extrude through various breaks in the chorion. The timing of adding oviducal jelly to the embryos was not critical for final chorion expansion. Delays up to 24 hr still resulted in chorion expansion. Controls without oviducal jelly never developed chorion expansion.

Oviducal jelly was prepared from lyophilized glands, frozen glands, and fresh glands. All three preparations were successful in some cases, but treatment with the lyophilized glands resulted in more consistent chorion elevation and in a low rate of bacterial infection. Frozen and fresh preparations were made by thinly slicing the gland, then mashing the slices in a small amount of seawater with a toothpick. The lyophilized preparation depended on preparing oviducal powder in advance of the cruise. The lyophilized oviducal gland was ground with a mortar and pestle, then sifted through a filter with a 0.2 mm pore size to remove large pieces of tissue; it was then stored in a freezer until needed. Sterile techniques (where possible) and the use of freshly filtered seawater not older than about 2 or 3 days are important procedures to prevent infection of the embryos.

Attempts to develop a technique in a systematic manner were hampered by a number of factors (see Discussion), which were unknown at the time, and therefore uncontrolled. During the course of this study, the basic method or protocol evolved to the state presented below (Figure 1). Times indicated are for experiments done at 22°C.

(1) A freshly caught gravid female squid is placed on a pan, the mantle opened and the ink sac removed. Eggs are obtained by cutting through the wall of an oviduct and extracting with a plastic spoon.

(2) One batch of eggs is flooded with seawater as a control to determine how rapidly the eggs hydrate. If hydration takes longer than 10 minutes, the subsequent technique should be modified by a second addition of sperm after hydration has occurred.

(3) The eggs are placed in a small pile in a 50 mm diameter plastic petri dish. The eggs have not been exposed to seawater at this point. The chorion in the ommastrephids examined did not adhere to the petri dish as it does in *Loligo pealei* (Klein & Jaffe, 1984).

(4) Sperm are removed from spermathecae (seminal receptacles) on the buccal membrane of the female squid by gently squeezing the base of the saclike spermathecae with a pair of forceps. The extruded sperm are confined by mucous covering the buccal membrane. This allows the sperm within a mucous strand to be transferred to the eggs with a pair of forceps.

(5) The mucous strand containing the sperm is gently dragged over the surface of the eggs causing the sperm mass to become thinly spread over the eggs. Sufficient water is transferred with the mucous to cause sperm motility. Often a few drops of seawater are added at this stage, and the petri dish is covered and allowed to stand for a few minutes.

(6) About 20–30 mg of lyophilized oviducal gland powder is mixed with 30 mL of 0.4 μm filtered seawater and vigorously stirred until a barely detectable increase in viscosity of the water (jelly-water) is noted.

(7) The jelly-water is added to the eggs and sperm so that a thin layer of this fluid covers the eggs. The fluid causes the eggs to spread out across the dish in a single layer.

(8) About 5 min after step 7, filtered seawater is added to half fill the petri dish.

(9) The petri dish is placed in an incubator at 22°C. Heat sterilization of the incubator prior to use is an important precaution.

(10) After about 3 hr, the successfully fertilized eggs are usually in the second or third cleavage, and the chorion should exhibit initial expansion. As a result, they can be easily recognized under a dissecting microscope. Developing embryos with elevated chorions are then transferred to freshly filtered seawater in another petri dish at a density of 10–15 embryos per dish.

(11) Often jelly-water is added once or twice again before organogenesis begins to insure chorionic expansion. This should be done within 24 hr of fertilization and is important if initial chorionic expansion did not occur. Changing of the seawater medium during embryogenesis is unnecessary since oxygen concentration does not seem to be a limiting factor in these circumstances.

(12) Hatching occurs in about 3 to 4 days at 22°C depending on the species.

RESULTS

We provide here results of tests concerning several phases of the artificial fertilization and rearing protocol and some initial results on hatchlings. Sperm from spermatophores, spermatangia (discharged spermatophores) attached to the female, and spermathecae were tested. All three sources provided sperm that successfully fertilized eggs; however,

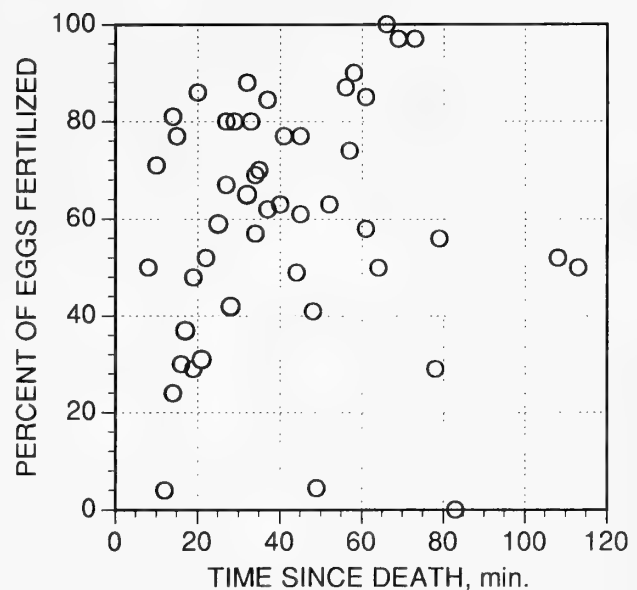


Figure 2

The effect of the time since death of the squid *Sthenoteuthis oualaniensis* on the ability of their eggs to be fertilized (fertilizability).

sperm from spermathecae were most reliable. Sperm became motile only in seawater. In both *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis*, sperm in spermatangia or spermatophores were difficult to separate from the matrix in which they were embedded. As a result, only sperm along the fringe of the cut edges became active in the seawater. Sperm from spermathecae were much easier to disperse and thus easier to expose to seawater. We timed the survival of motile sperm; activity was greatly reduced after 15 min and completely stopped after 25 min (approximately 24°C).

In 49 fertilization trials on *Sthenoteuthis oualaniensis*, where the percent of eggs fertilized was counted, a mean of 60.6% (24.8% standard deviation) of the eggs were successfully fertilized, and the median was 63% (range 0–100%).

Eggs removed from the oviducts of *Sthenoteuthis oualaniensis* did not have smooth rounded surfaces. Rather, they appeared like a slightly deflated ball with a number of indentations. When the eggs were placed in seawater, these indentations gradually disappeared. Since this process occurred in the presence of seawater, we term it “hydration,” although the mechanism involved in the rounding of the chorion is unknown. Ten attempts were made to fertilize eggs that were not hydrated, and none could be fertilized. In the single *Ommastrephes bartramii* examined for hydration, over 90% of the eggs were hydrated after 2 min in seawater. While the fastest time to 90% hydration that we have measured in *S. oualaniensis* was also 2 min, hydration time was highly variable in this species. On one occasion, hydration of all eggs was incomplete after nearly

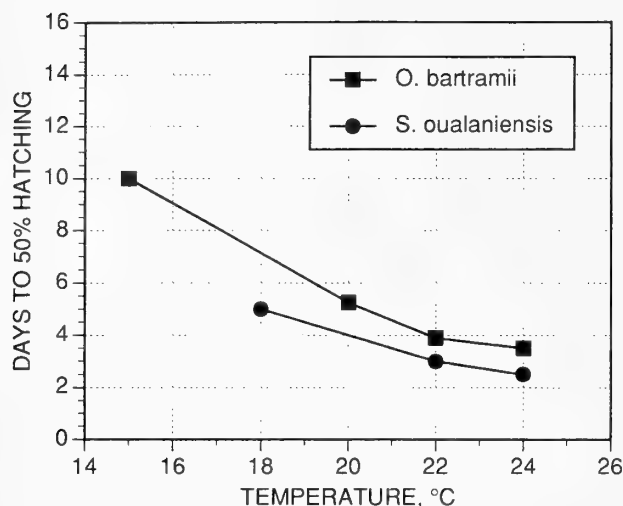


Figure 3

Time to 50% hatching of artificially fertilized eggs of *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* plotted against incubation temperature.

40 min, and a few had not hydrated after 9 hr in seawater. Most of these eggs did not fertilize (fertilization success was less than 5%). The eggs came from a 200 mm mantle length (ML) female whose oviducts were estimated to be one-third to one-half full. From another female of the same length but with oviducts about two-thirds full, less than 10% of the eggs hydrated in 10 min after seawater was added. Fertilization was not attempted in this case. We have examined hydration times in only five other *S. oualaniensis* females. Their hydration times in minutes (i.e., time taken to hydrate 90% of the eggs) were: 9, 2, 7, 15, and 4.

Eggs in the oviducts of dead female squid with open mantles remain viable for some time. We attempted to fertilize eggs from *Sthenoteuthis oualaniensis* up to nearly 2 hr past death and, within this time frame, we found no clear effect of the "age" of the eggs on their ability to be fertilized (Figure 2). In these cases, the mantle of the female squid was cut open immediately after death to allow free aeration of the oviducts. Peristaltic action of the oviducts continues for some time after death, which may also aid in continued aeration of the eggs. We have no data on whether or not developmental abnormalities might be related to the age of the eggs. As a general practice, however, fertilizations were performed within one hour of the death of the female.

We used the powder of lyophilized oviducal gland from the ommastrephids *Todarodes pacificus*, *Sthenoteuthis oualaniensis*, and *Ommastrephes bartramii* to stimulate chorion expansion among species. All nine possible combinations of eggs and powder between these three species (e.g., *T. pacificus* powder used to make jelly-water that is applied to eggs from *S. oualaniensis*) resulted in chorion expansion.

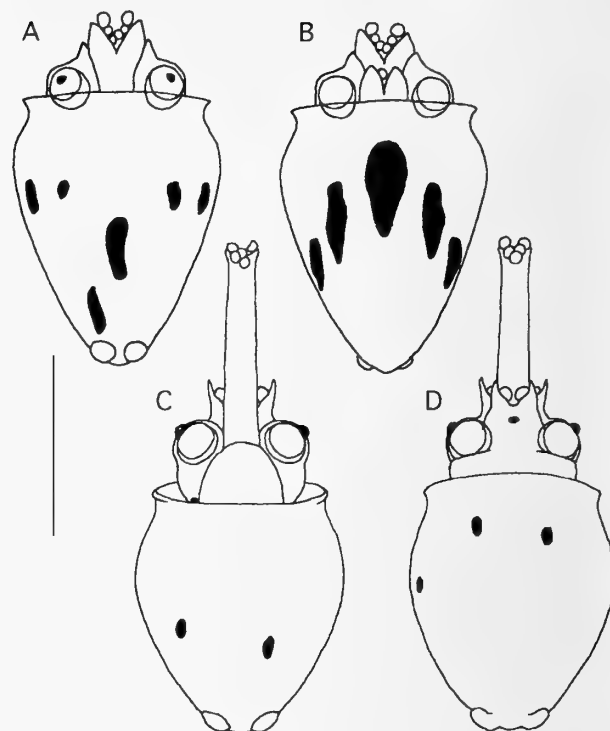


Figure 4

A, B. *Ommastrephes bartramii*. Ventral and dorsal views of a 2-day-old hatchling from an artificially fertilized egg showing chromatophore pattern. Although this is the same age as the hatchling in Figure 5F, G, it is not as advanced in development as the latter presumably due to premature hatching. Note the pair of enlarged proboscis suckers and short proboscis. C, D. *Sthenoteuthis oualaniensis*. Ventral and dorsal views of a 4-day-old hatchling from an artificially fertilized egg showing chromatophore pattern. Note equal sized proboscis suckers and length of the proboscis. Bar = 1 mm.

In spite of considerable variability in success rates, hundreds of embryos of *Ommastrephes bartramii* and *Sthenoteuthis oualaniensis* were hatched. Initial tests on the effect of temperature on the hatching time have been made with the objective of determining the optimum temperature range for development (Figure 3). Ultimately, such information can supply clues to the spawning depths and latitudes of the squids in nature. The time at which 50% of the embryos hatched was used as a measure of the hatching time. The offset between the two species may be due to the differences in their egg sizes. Most eggs of *O. bartramii* measured about 0.92×1.10 mm, although some eggs were much larger (1.25×1.10 mm). The larger eggs, which accounted for nearly half of the eggs in some females and virtually none in other females, could not be fertilized. In *S. oualaniensis*, eggs of only one size were present, and they measured 0.84 mm \times 0.70 mm. Over the temperature range examined, the duration of embryonic development through hatching decreased with increasing temperature (Figure 3). Although there is an apparent change in the slope of the

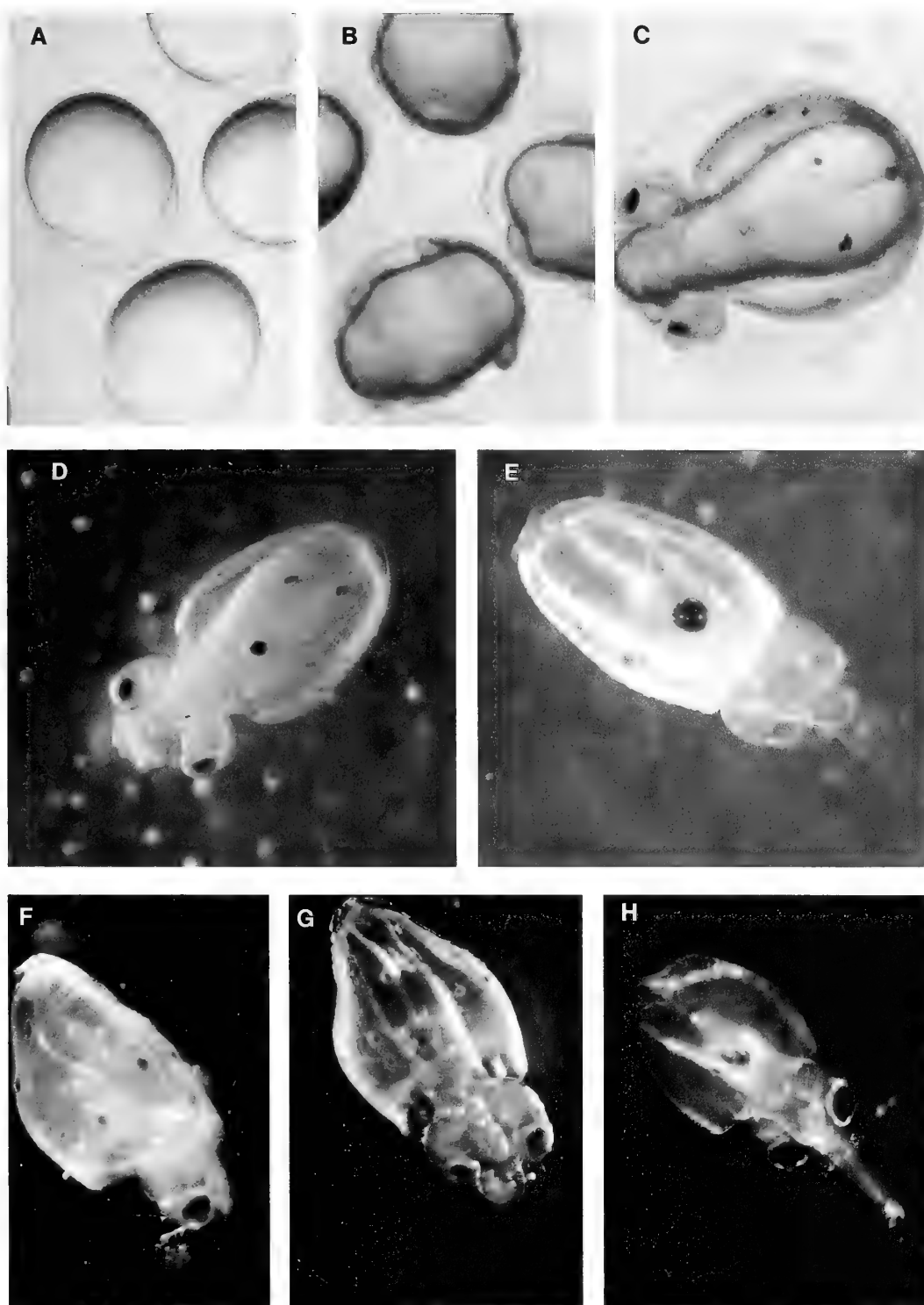


Figure 5

Ommastrephes bartramii embryos and hatchlings from artificially fertilized eggs. A. Approximately stage 14 of Arnold (1990). Shows initial chorion elevation. B. Approximately stage 20 of Arnold (1990). Shows only partial secondary expansion of chorion. C. Just prior to hatching with chorion only partially elevated. D. Just after hatching. Note large internal yolk sac. E. 1-day-old hatchling. Side view showing slightly elongate proboscis. F. 2-day-old hatchling. Side view showing reduced internal yolk sac. G. 2-day-old hatchling. Ventral view showing elongate proboscis and absence of internal yolk. H. 4-day-old hatchling. Ventral view showing elongate proboscis and absence of internal yolk.

curve for *O. bartramii* at 22°C, we could not determine the upper temperature optimum from this limited data.

Hatchlings have been kept alive up to 6 days in 250 ml of filtered seawater in glass bottles placed on a plankton rotator. Several attempts were made to feed 2- and 3-day-old hatchlings by adding a known number of small copepods of the genera *Oithona* and *Clausocalanus*, fish eggs, and squid eggs to the culture bottles. None of the potential prey were eaten. This lack of first feeding may reflect wrong prey items, inappropriate conditions for maintaining the paralarvae, or insufficient development of the hatchlings.

At hatching, the paralarvae have a very short proboscis and a large internal yolk supply (Figure 5C). By 4 days post hatching, the yolk sac is nearly gone, the proboscis has elongated greatly, and the eyes are more fully developed (Figure 5D-G). After 4 or 5 days at 22 to 24°C, the squid begins to deteriorate due to starvation. The 2-day-old hatchling of *Ommastrephes bartramii* exhibited the same chromatophore pattern on the mantle (Figure 4) as that previously described for very young (1.6 mm ML) paralarvae (Young & Hirota, 1990). No chromatophores, however, were present on the head of the hatchlings. The proboscis had enlarged lateral suckers (approximately 1.5 times the diameter of the medial suckers) as is characteristic for this species. In contrast, the 4-day-old *Sthenoteuthis oualaniensis* lacked the posteroventral chromatophores, although the suckers on the proboscis had their characteristic uniform size.

DISCUSSION

The fertilization technique we used placed sperm on the ova before the latter were capable of being fertilized due to lack of hydration. Because sperm motility decreases after approximately 15 min, the possibility exists that the sperm will become immobile before the ova are hydrated. Nevertheless, the technique generally resulted in good fertilization rates. Perhaps sperm from the center of the spread sperm mass become progressively activated as the mass dissipates, resulting in a constant new supply of sperm over a prolonged period. Presumably, timing mismatches between egg hydration time and sperm immobility in this step are responsible for some of the variability encountered. This potential problem can be avoided by hydration of the eggs first, followed by concentrating eggs at one side of a tilted petri dish, decanting off most of the seawater, then adding sperm. This method resulted in successful fertilization; however, because the eggs are already in seawater, they no longer provide the resistance needed to help spread the sperm mass, and the eggs are more difficult to coat with jelly. We preferred to risk a possible timing mismatch.

While the technique described here resulted in successful hatching of embryos, it still has not reached the level of refinement where it can be relied on for obtaining large numbers of hatchling squids on a regular basis. Improvement is still needed in the following areas:

(1) A more consistent method is needed for obtaining chorion expansion. The next step in this direction would be to prepare a range of oviducal jelly solutions of different viscosities and from the glands of different individual females. Since fertilization is not necessary for chorion expansion, the solutions could be quickly tested on batches of unfertilized eggs for initial chorion expansion. The solution producing the best result would then become the stock solution for subsequent fertilizations. The ultimate step in this direction, of course, would be to extract the specific chemicals that trigger chorion elevation from the oviducal gland so that standard solutions could be prepared.

(2) A good method is needed for preventing infection. Sterile technique where possible and low-density cultures help greatly, but insurance is needed from appropriate antibiotics that will not interfere with embryogenesis.

(3) We have noted variable, but sometimes frequent, occurrences of developmental abnormalities (e.g., inverted mantles) and occasional cessation of development during the early stages of embryogenesis. One possible cause of such problems could be the rolling of embryos in the petri dishes due to the ship's motion. In many cases, rolling is retarded by the jelly but it can be highly variable. One way to preventing rolling would be to position each embryo onto openings of pieces of nitex plankton netting placed on the bottom of the petri dishes.

(4) An effective method for releasing sperm from their matrix within spermatangia is needed. In general this would provide a larger supply of sperm for fertilizations. It would be especially useful for species that lack spermathecae.

ACKNOWLEDGMENTS

We thank the officers and crews of the *Hokusei Maru*, *Moana Wave*, and *Wecoma* for their assistance at sea, and the many volunteers that helped with the cruises. We also thank J. M. Arnold, University of Hawaii, for reviewing the manuscript.

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Hatching of *Nautilus belauensis* Saunders, 1981, in Captivity: Culture, Growth and Stable Isotope Compositions of Shells, and Histology and Immunohistochemistry of the Mantle Epithelium of the Juveniles

by

S. OKUBO¹, T. TSUJII¹, N. WATABE², AND D. F. WILLIAMS³

Abstract. A single female of *Nautilus belauensis* laid 43 eggs in the Shima Marineland Aquarium, Japan, from October 1987 through December 1988. Three of the eggs maintained at an average 24.4°C hatched, and the hatchlings (designated nautilus A, B, and C) survived 32 to 73 days. Nautilus A, B, and C had shell diameters of 3.24, 3.30, and 3.18 cm, respectively, a few days after hatching, which increased to 3.70, 3.86, and 3.29 cm at death. The number of septa is 11 in B and 10 in C. A narrowing of the angular distance occurred between septa 6 and 7 in B and 7 and 8 in C and thereafter until death. The nepionic constriction is present in the body chamber of both shells. Hatching is estimated to have occurred after the formation of septum 9. The $\delta^{18}\text{O}$ values of septa show an overall average close to zero both in B and C. The $\delta^{13}\text{C}$ profile undergoes a dramatic 4‰ negative shift in septa 6 and 7 in B and in septa 4 through 6 in C. The shift may have been caused by partial ingestion of egg capsules by the embryos prior to hatching. The $\delta^{13}\text{C}$ of septa 1-3 and 8-10 or 8-11 is close to the inferred $\delta^{13}\text{C}$ of dissolved CO_2 of the culture water. The estimated average rate of apertural growth is 0.20 mm/day in B and 0.28 mm/day in C. The soluble and insoluble proteins of the shell matrix are separated into three to four fractions by SDS gel electrophoresis. Immunohistochemical analysis shows that synthesis and secretion of the soluble and insoluble shell matrix occur in the outer mantle epithelium away from the mantle edge.

INTRODUCTION

Nautilus inhabit obscure habitats scattered throughout the Indo-Pacific seas at depths ranging from near the surface to greater than 600 meters (Saunders & Ward, 1987; Ward, 1987). Most of the work to date on the biology and ecology of *Nautilus* is based on adults because of the relative ease of studying captured and preserved specimens. However, research on reproduction, embryonic development, or em-

bryonic and juvenile shell formation is impaired by difficulty in rearing and raising nautilus in captivity. Such a capability would make it possible to obtain ontogenetic information, knowledge about survival, and the ability to distinguish embryonic and juvenile fossils of this and extinct groups of ammonoids and nautiloids. It is therefore significant that several aquaria, e.g., Shima Marineland (Okubo, 1989), Kamoike Aquarium (Tanabe et al., 1991), Waikiki Aquarium (Carlson, 1991; Carlson et al., 1992), and Toba Aquarium (Uchiyama, 1993) have succeeded in rearing *Nautilus belauensis* Saunders, 1981, or *Nautilus macromphalus* Sowerby, 1849, in captivity, resulting in publication of a number of papers on ontogenetic development and embryonic and juvenile shell structures of these species (e.g., Carlson, 1985; Arnold & Carlson, 1986; Arnold, 1987, 1992; Arnold et al., 1987, 1990; Landman & Cochran, 1987; Landman et al., 1989, 1994).

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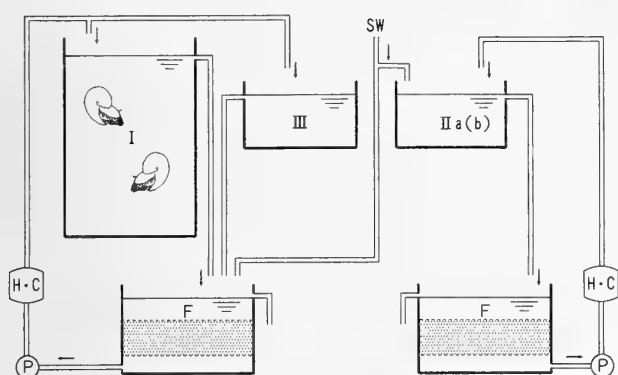


Figure 1

Diagram of the aquarium system for *Nautilus* at the Shima Marineland Foundation. Not to scale. I: adult holding tank. II: egg holding tank. Two identical tanks, IIa or IIb, are provided. III: juvenile holding tank. F: filter. P: pump. H-C: heating and cooling unit. SW: ambient seawater.

In Shima Marineland, three individuals hatched out from eggs laid in the Marineland's aquaria and survived 32 to 73 days. The total period of culture from the egg-laying to death was around 400 days. A brief account of this culture has been reported by Okubo (1989). The present paper reports further the culture methods, some histological and immunohistochemical characteristics of the mantle, as well as stable isotopic composition of the shells.

MATERIALS AND METHODS

Adult *Nautilus belauensis* Saunders, 1981, were captured in late June 1987, off the Palau Islands in the Pacific Ocean by members of the Toba Aquarium, Japan, and were immediately transported to Japan by air. From those specimens, the Shima Marineland Foundation received one female and two males on 4 July 1987. They were kept in a closed system glass aquarium I (85 × 60 × 90 cm) (Figure 1). Natural seawater was used for the culture, and the temperature was maintained at 18.3°C. The animals were fed defrosted frozen shrimp, *Penaeus* sp., *ad libitum*. The female started egg-laying 5 October 1987. Two days through 2 months after laying, a total of 13 eggs were transferred to aquarium IIa, and a total of 30 eggs were transferred to aquarium IIb (Figure 1). Three nautilus, designated A, B, and C, hatched out in aquarium IIa. Four days (nautilus A and C) and 5 days (nautilus B) after hatching, they were transferred into aquarium III (Figure 1). The average water temperatures during the culture are shown in Table 1. The animals were fed the shrimp *Palaeomon* or medaka (*Oryzias latipes*). At intervals, shell diameters and breadths were measured with calipers. Nautilus B and C were available for septal spacing measurements, stable isotope analysis, and mantle histology after their death.

Table 1

Water temperatures in °C during the culture period.

	Average	Maximum	Minimum
Adult			
7/87-1/89	18.3		
13 Eggs (Aquarium IIa)			
10/5/87-5/27/88	18.3		
5/28/88-5/31/88	19.4	19.8	19.0
6/1/88-6/30/88	21.0	22.0	20.0
7/1/88-7/31/88	23.6	25.4	21.8
8/1/88-8/31/88	25.2	27.4	23.5
9/1/88-9/30/88	25.3	26.0	24.8
10/1/88-10/3/88	24.5	24.6	24.4
10/4/88-10/31/88	24.4		
11/1/88-11/30/88	24.5	24.6	24.4
12/1/88-12/27/88	24.3	24.8	23.2
1/1/89-1/4/89	23.5	23.6	23.4
30 Eggs (Aquarium IIb) (no hatching)			
1/13/88-1/90	18.3		
3 Juveniles			
12/28/88-12/31/88 ^{1,2}	23.4	23.8	23.2
1/4/89-1/8/89 ³	23.5	23.6	23.4
1/1/89-1/31/89 ^{1,2,3}	18.4	18.8	18.0
2/1/89-2/28/89 ^{1,2,3}	18.3	18.8	17.8
3/1/89-3/10/89 ²	17.9	18.3	17.7

¹ Nautilus A; ² Nautilus B; ³ Nautilus C.

Oxygen and Carbon Stable Isotope Analyses

The shells of nautilus B and C were cut longitudinally in half. Right halves slightly off from the median plane and without siphuncles were available for the isotope analyses. Shells were cleaned briefly with 6% sodium hypochlorite, rinsed with distilled water, and a few mg of shell material were removed from each septum with a micro-drill. The method of analysis followed standard procedures as described by Williams (1984). After the organic material was removed from the samples by roasting at 380°C *in vacuo*, the carbonate was reacted with 100% phosphoric acid, and evolved CO₂ was introduced into a mass spectrometer (VG Isogas SIRA 24) after cleaning of contaminant H₂O by fractional freezing. The isotope ratios were expressed as δ¹⁸O and δ¹³C values in per mil (‰) relative to CO₂ from the PDB standard as follows:

$$\delta^{18}\text{O} = \left(\frac{{}^{18}\text{O}/{}^{16}\text{O} \text{ of samples}}{{}^{18}\text{O}/{}^{16}\text{O} \text{ of standard}} - 1 \right) \times 1000.$$

$$\delta^{13}\text{C} = \left(\frac{{}^{13}\text{C}/{}^{12}\text{C} \text{ of samples}}{{}^{13}\text{C}/{}^{12}\text{C} \text{ of standard}} - 1 \right) \times 1000.$$

For comparison, δ¹³C of organic materials of egg capsules of nautilus B, of an embryo that did not hatch out, and of *Nautilus pompilius* laid 29 July 1992 (Okubo & Tsujii, unpublished) was analyzed as follows: a small piece of dried capsule (carbonate-free) was lightly ground, and

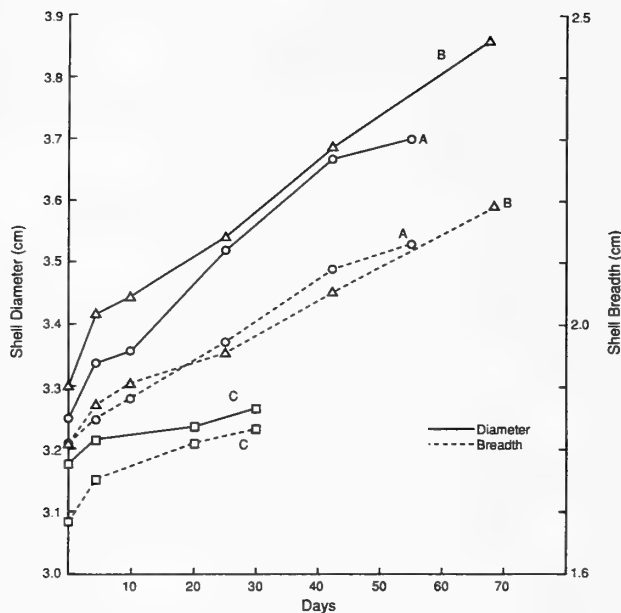


Figure 2

Growth of shell diameters (left ordinate) and shell breadth (right ordinate) of juveniles of nautilus A (A), nautilus B (B), and nautilus C (C) during the culture periods (abscissa).

combusted in a Perkin-Elmer C-H-N Analyzer. CO₂ gas from the combustion was purified with water and analyzed in the mass spectrometer.

Immunohistochemistry

For antisera preparation, pieces of an adult shell of *Nautilus belauensis* were powdered and decalcified in 0.5 M K-EDTA in 0.05 M NH₄CO₃ buffer. Insoluble and soluble organic matrices were isolated following the method of Watabe et al. (1991). Total soluble or insoluble matrix proteins were used as antigens to produce anti-soluble or anti-insoluble matrix antisera, respectively, in male New Zealand white rabbits. The matrix proteins were analyzed by SDS-PAGE as follows: the insoluble and soluble matrix preparations were treated with 1% chitinase (enzyme/substrate) and 1% chondroitinase (enzyme/substrate), followed by partial solubilization in n-butanol, homogenized with 8 M guanidine-HCl containing 10% β-mercaptoethanol and 0.1 M tris-HCl, pH 7.5, and then dialyzed against 6 M urea-2 M thiourea mixture containing 0.17% β-mercaptoethanol (Watabe et al., 1991). The dialyzate was subjected to 12% SDS-PAGE following the method of Laemmli & Favre (1973). Identification of antigenic proteins of the antisera was performed by the standard Western blot method (Towbin et al., 1979).

Nautilus B and *C* were fixed postmortem in Zamboni fixative (Zamboni & DeMartino, 1967) or in 10% buffered

formaldehyde, respectively, at room temperature. The soft bodies were dissected out, dehydrated in a series of ethanol, and embedded in paraffin. Serial sections were cut approximately 3 μm thick and stained with hematoxylin and eosin for general microscopy. For the PAP (horse radish peroxidase-antiperoxidase) immunostaining, sections were deparaffinized and incubated with anti-soluble or anti-insoluble matrix antisera for 20 min at room temperature, followed by treatment with PAP (Universal DAKO PAP KIT™, Dako, Santa Barbara, California, USA). Preimmune serum was used as the primary antiserum for control.

RESULTS

Egg-Laying and Juvenile Culture

The single female laid a total of 43 eggs, from 5 October 1987, until 28 December 1988, on glass walls, between the coral branches and slates at the bottom of aquarium I. The 30 eggs (Figure 7) which were transferred from aquarium I to aquarium IIb (Figure 1) and maintained at 18°C did not hatch. However, approximately 1 year from the egg-laying, three eggs hatched in aquarium IIa maintained at an average 24.4°C. The adult female died January 1989. *Nautilus A* and *B* hatched out on 27 December 1988, and *C* on 4 January 1989. They were kept at water temperatures of 23.4–23.5°C for the first 3 days (*nautilus A, C*) or 4 days (*nautilus B*), transferred to aquarium III (Figures 1, 9), and maintained at an average temperature of 18.3°C (maximum 18.8°C, minimum 17.7°C). (It was discovered on 7 November 1988, more than 2 months before hatching, that an upper portion of the egg capsule of *nautilus C* had opened and a part of the shell was visible through the opening (Figure 8).) *Nautilus A* survived for 60 days after hatching, or 438 days after egg-laying; *B* survived for 73 days, or 442 days; and *C* for 32 days, or 413 days.

A few days after hatching, the shell diameters of *nautilus A, B*, and *C* were 3.24, 3.30, and 3.18 cm, respectively. Each increased to 3.70, 3.86, and 3.29 cm, respectively, during the culture periods (Figure 2). Comparatively, the initial shell breadths in *A, B*, and *C* of 1.8, 1.8, and 1.68 cm increased to 2.13, 2.19, and 1.87 cm, respectively (Figure 2). The average daily growth rate of shell diameter was 0.77 mm or 0.2% of the original diameter in *A* and *B*, and 0.34 mm or 0.1% in *C*. The average daily growth rate of the shell breadth was 0.55 mm or 0.3% in *A*, 0.53 mm or 0.3% in *B*, and 0.59 mm or 0.3% in *C*. The growth rates of shell diameter of *A* and *B* and shell breadth of *B* and *C* dropped to almost half after the first 5–10 days. In *A*, the growth rate of the breadth did not change appreciably until the last 10 days of lower rate. In *C*, the growth rate of the diameter dropped to nearly one-third after the first 5 days, and the lower rate continued during the rest of the culture.

The number of septa is 11 in *B* (Figure 3b) and 10 in *C*, and that of chambers 12 in *B* and 11 in *C* (Figure 4b).

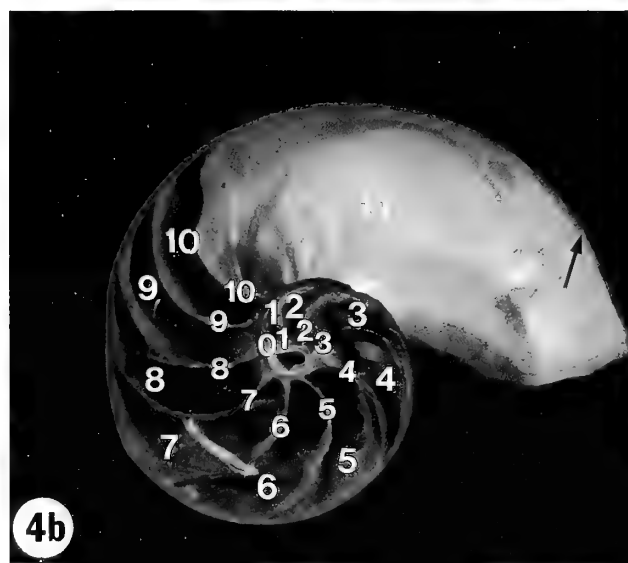
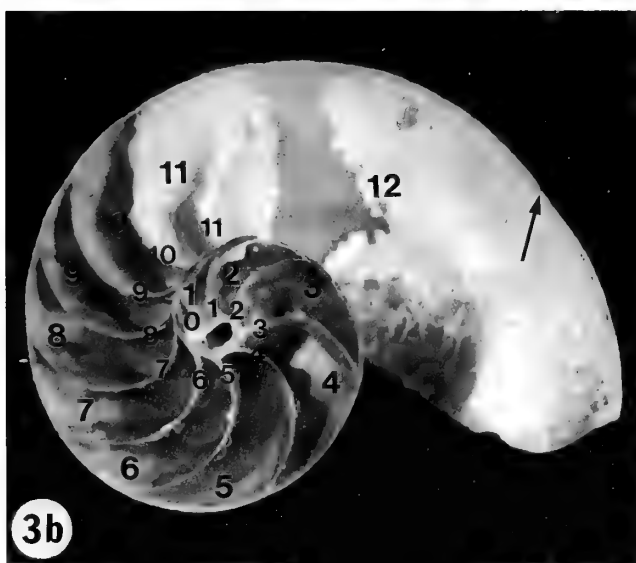
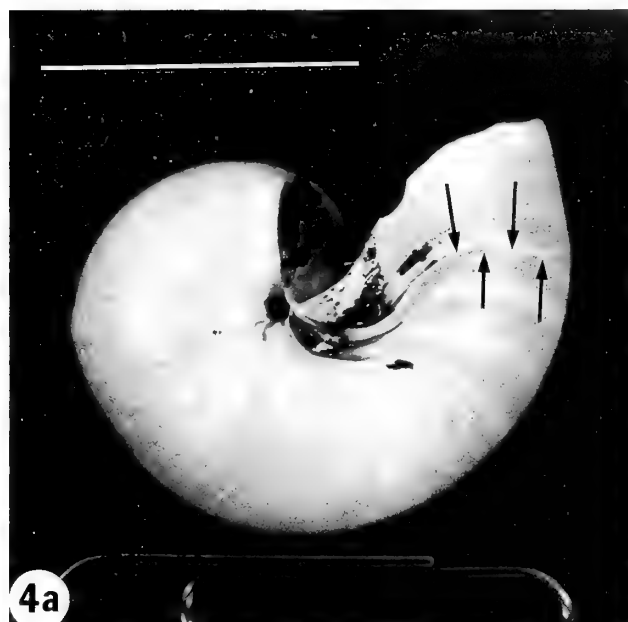
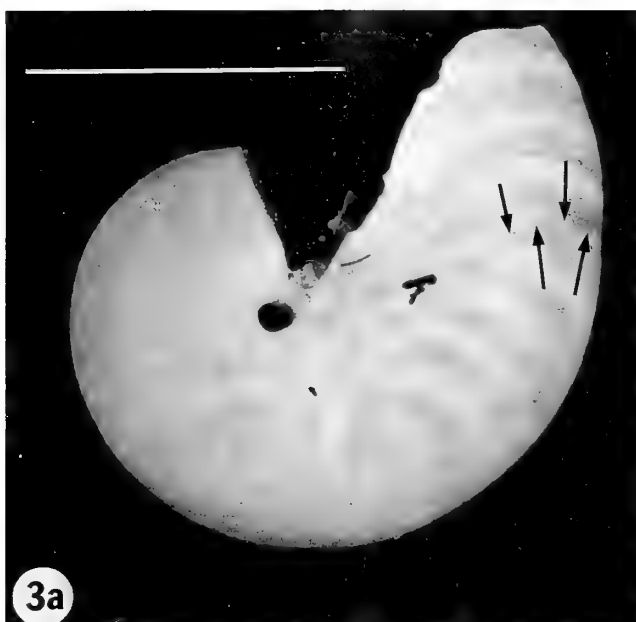


Figure 3a, 3b

Same magnifications. Shell of juvenile nautilus B. Arrows point to the nepionic constriction. Small numbers indicate septum numbers. Large numbers are chamber numbers. Bar = 2 cm.

Figure 4a, 4b

Same magnifications. Shell of juvenile C. Arrows point to the nepionic constriction. Small numbers indicate septum numbers. Large numbers are chamber numbers. Bar = 2 cm.

Decrease in septal spacing occurs between septum 6 and 7 in B and 7 and 8 in C and afterward until death (Table 2). A distinct constriction is observed in both shells in the last (body) chamber at a little over $1\frac{1}{4}$ whorls from the apex. The shell diameter at the constriction is 33.0 mm and 31.8 mm in B and C, respectively. The shell shape of C deviates from a normal log spiral and appears to be

deformed. Black layers are present immediately before and after the constriction in C (Figure 4a).

Oxygen and Carbon Stable Isotope Ratios

The stable isotope profiles of the nautilus shell B and C are very similar in average isotopic composition (Figure 5). The shell of B has nearly a 6‰ range in $\delta^{18}\text{O}$ and a

Table 2

Spacing between septa in angular distance (in degrees) in nautilus B and C.

Septum number	Chamber number	Nautilus B	Nautilus C
0-1	1	45	50
1-2	2	45	48
2-3	3	47	48
3-4	4	45	43
4-5	5	45	43
5-6	6	42	42
6-7	7	27	42
7-8	8	25	25
8-9	9	25	25
9-10	10	25	25
10-11	11	25	

5‰ range in $\delta^{13}\text{C}$. The $\delta^{13}\text{C}$ profile undergoes a dramatic 4‰ negative shift at septa B-6 and B-7. From septa B-8 through B-11, the $\delta^{13}\text{C}$ profile remains fairly constant and is close to the inferred $\delta^{13}\text{C}$ of dissolved CO_2 of the culture water. The $\delta^{18}\text{O}$ profiles show no systematic change except for a very positive value for septum B-8.

The shell of C has nearly the same range in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values as the shell of B. The $\delta^{13}\text{C}$ profile shows little variation in the first three septa and then an abrupt 4‰ negative shift. From septa 4 through 6, the $\delta^{13}\text{C}$ values are very similar but significantly depleted, similar to the pattern seen in shell B. From the eighth through the last septum in shell C, the values show some variability but have an average composition close to the inferred $\delta^{13}\text{C}$ of dissolved CO_2 of the culture water. The $\delta^{18}\text{O}$ profile of C shows a slight positive trend from septum 1 through 8 but has an overall average close to zero, similar to shell B.

The $\delta^{13}\text{C}$ of the organic egg capsules of B and those of two other embryos are almost identical and show negative values of $-14.8 \pm 0.05\text{‰}$.

Immunohistochemistry

By 12% SDS-PAGE, the adult shell insoluble matrix was fractionated into clear protein bands of 76, 66, and 48 KD (Figure 6a). The soluble matrix was fractionated into a clear band of approximately 150 KD and faint bands of 76, 66, and 50 KD (Figure 6a). The anti-soluble and anti-insoluble matrix antisera showed specificity for the insoluble 76 and 48 KD proteins, and soluble 150 KD protein, respectively (Figure 6b).

The mantle of the juvenile nautilus consists of the outer epithelium, connective tissue, and the inner epithelium (Figures 10, 11). The mantle edge is branched into three folds: the outer, middle, and inner fold. The outer epithelial cells are columnar and tallest near the base of the outer mantle fold and gradually decrease in height aborally (Fig-

ures 10, 11). The nuclei are elongated and occupy centro-basal regions of the cells (Figures 10-14). Some faintly stained granules are present in supranuclear regions of the cytoplasm (Figure 12).

Sections incubated with the anti-soluble matrix anti-serum and stained with PAP show distinct red color reaction products in the outer epithelial cells (Figures 11, 13). The cells of the outer mantle fold show very little reaction. The stained and little-stained regions are clearly separated (Figure 11, arrow), and the tall outer epithelial cells mark the apertural end of the stained region. The staining products are in the form of granules and distributed in the apical regions of the outer epithelial cells between the nucleus and the cell surface (Figure 13). The cell surface shows the strongest reaction. The middle and inner mantle folds and the inner epithelium also show very little reaction, and no reaction is found in the connective tissue.

The reaction with the anti-insoluble matrix serum is also distinct in the outer mantle epithelium (Figure 14), and the localization of stained cells (not shown) is the same as in the anti-soluble matrix. However, the reaction products are lighter in color than those with the anti-soluble matrix serum, and the products are distributed mainly in the supranuclear regions.

The control sections show no reaction (Figures 10, 12). No difference was found in the localization of PAP staining products between the fixation with Zamboni's fixative and buffered formaldehyde except that the products appeared to be denser in the Zamboni's fixative.

DISCUSSION

In the present culture, those eggs kept at 25°C for an extended period hatched, but those kept at 18°C did not. These results conform to previous reports that higher temperatures are favorable for hatching (Ward, 1987; Carlson et al., 1992). Even so, the hatching rate was only three out of 13 eggs. Many factors affect nautilus physiology in aquaria (Carlson, 1987; Kanie et al., 1979; Kawamoto et al., 1980), and more experiments are needed to establish the optimum temperature and other culture conditions.

Research on development of hatched juveniles of nautilus in commercial aquaria is limited because handling of the animals must be kept to a minimum in order to keep them alive as long as possible for the exhibit. Even the dead shells are often preserved for display. In spite of those limitations, the present results show some pertinent data on the growth of juvenile shells. It should be mentioned, however, that the data presented here are based on measurements or observations of two or three specimens, and no statistical comparisons with the published data are possible.

The average daily growth rate of the shell diameter of nautilus A and B was 0.77 mm, and that of C was 0.34 mm or about half of that of A and B. Specimen C shows shell deformation and black layers indicative of an un-

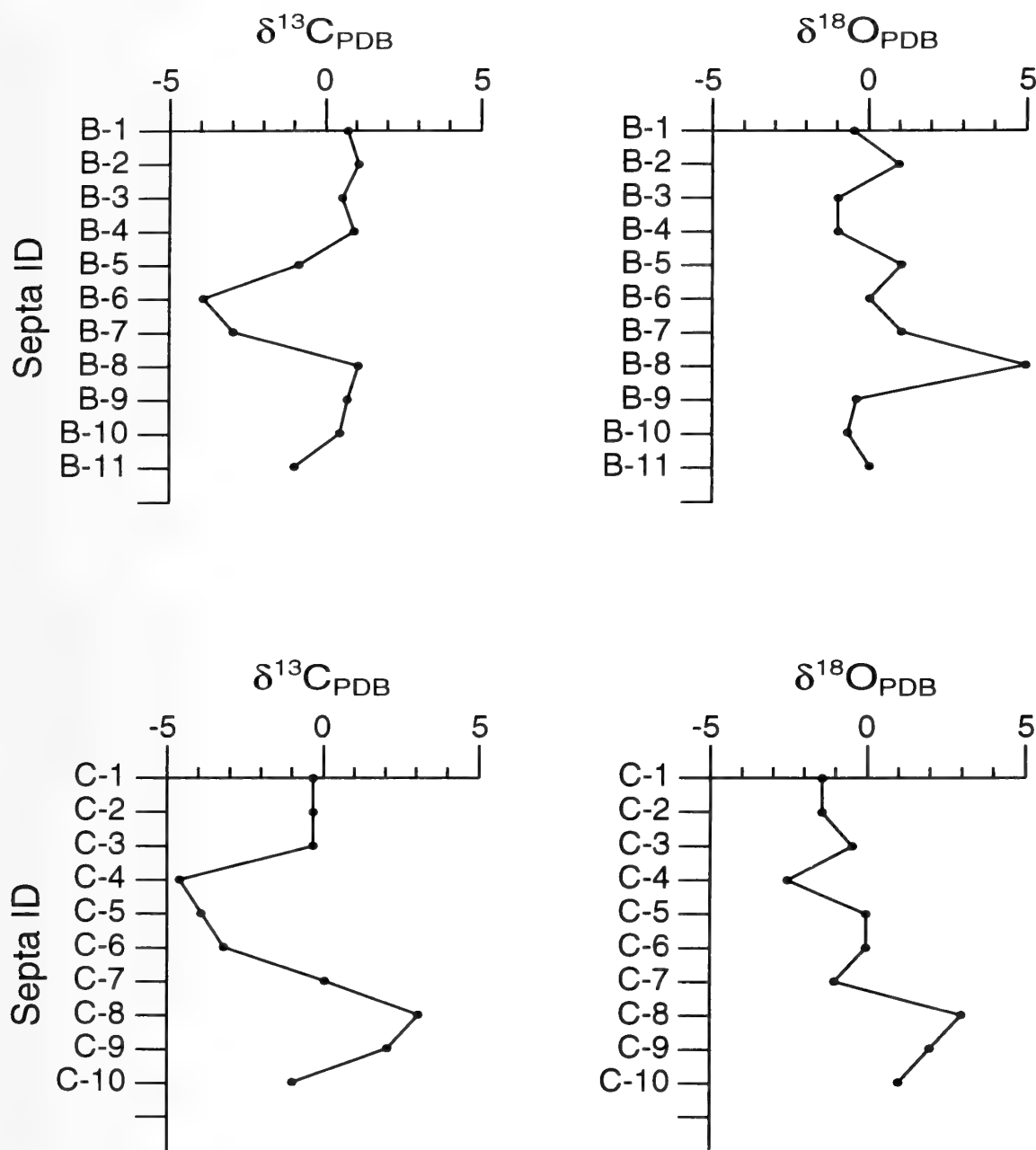


Figure 5

Stable isotope profiles of the nautilus shell B (top two graphs) and C (bottom two graphs).

healthy condition of the animal (Arnold, 1985; Arnold et al., 1987). In fact, this animal lived only half as long as A or B. The average rate of aperture growth from hatching to death was 0.20 mm/day in B and 0.28 mm/day in C. Immature specimens of *Nautilus belauensis* showed the highest rate of 0.12 mm/day with an average of 0.1 mm/day reported by Saunders (1983) and 0.1 to 0.14 mm/day

by Landman & Cochran (1987). The average rate reported in mature *Nautilus macromphalus* kept in an aquarium at 16°C was 0.15 mm/day (Ward et al., 1981), and 0.14 mm/day at less than 20°C (Kanie et al., 1979). The rates obtained in the present study are similar to those of 0.2–0.22 mm/day in small immature specimens of *Nautilus pompilius* reported by Landman & Cochran (1987) and

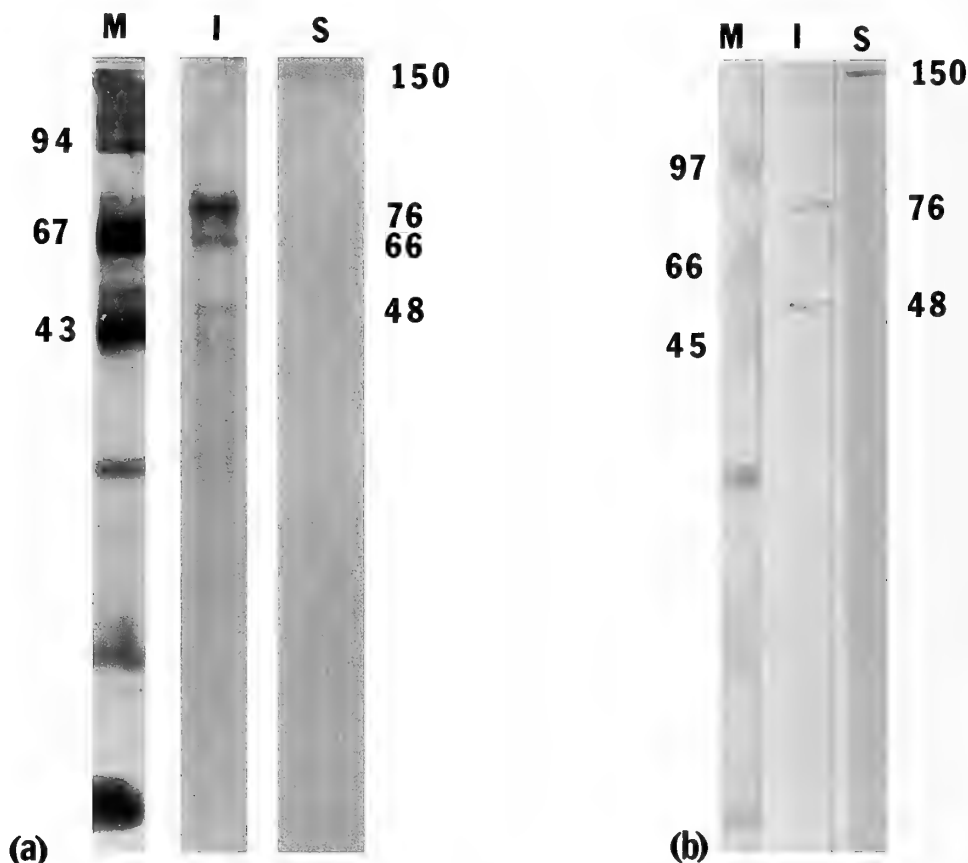


Figure 6

(a). 12% SDS polyacrylamide gel of insoluble (I) and soluble (S) shell matrices from an adult *N. belauensis*. M: marker. The numbers indicate kilodaltons.

(b) Immunoblot analysis of anti-insoluble (I) and anti-soluble

(S) matrix antisera. M: marker. The numbers indicate kilodaltons. (150 is for the soluble; 76 and 48 are for the insoluble matrix.)

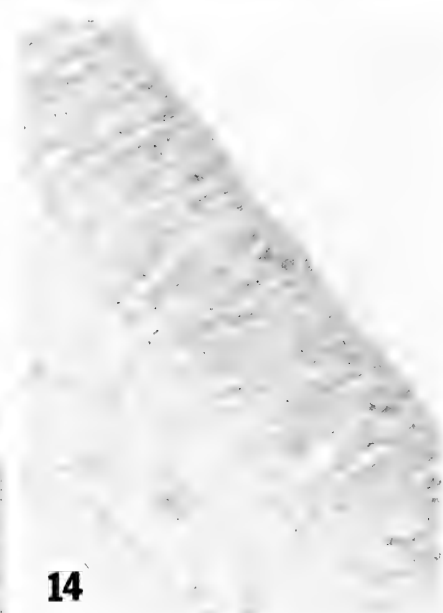
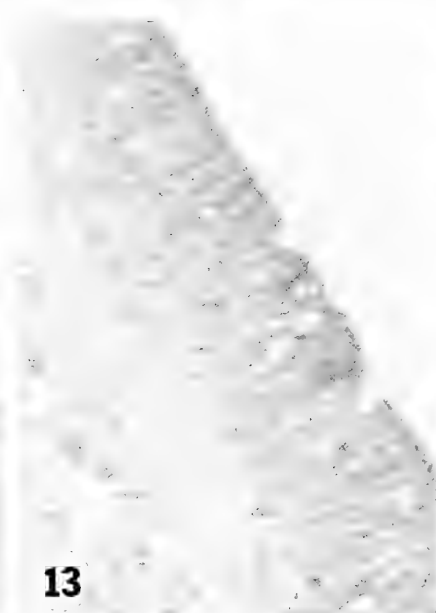
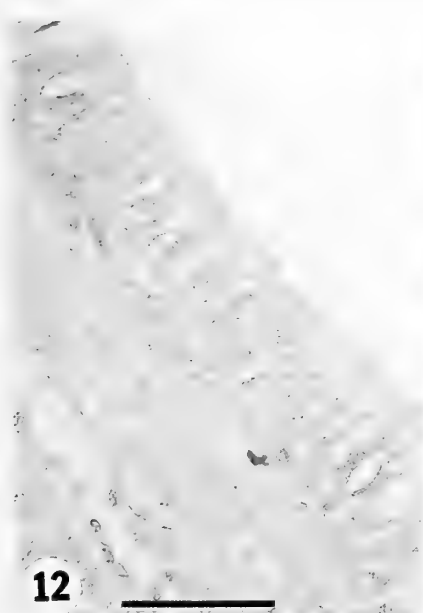
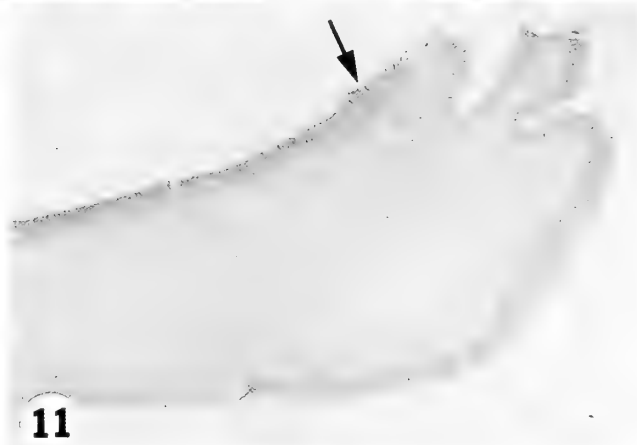
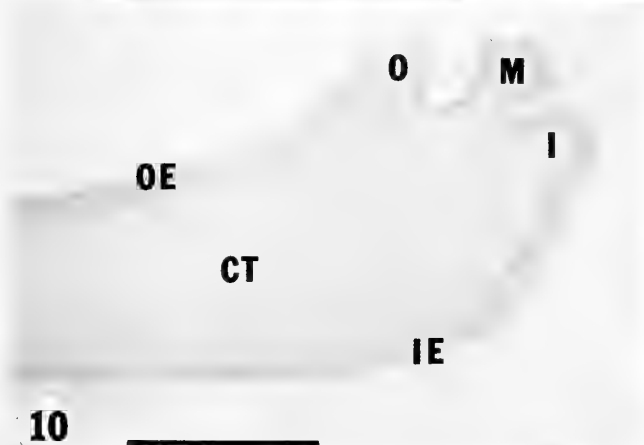
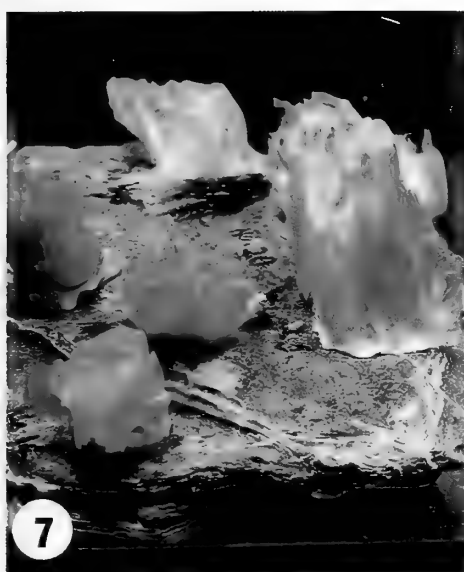
of 0.25 mm/day in *N. macromphalus* at 22–27°C (Martin et al., 1978), but lower than that of *N. macromphalus* obtained at the Noumea Aquarium in New Caledonia (0.54 mm/day) or that of *N. belauensis* in Waikiki Aquar-

ium (0.42 mm/day) (see Carlson et al., 1992). However, statistical significance of those similarities and differences is unknown as stated previously.

Frequently observed features of juvenile nautilus shells

Figures 7–14

Figure 7. Eggs (3–4 cm tall) laid on slates of aquarium I and transferred to IIb. Figure 8. Nautilus C embryo in the partially opened egg capsule. The photograph was taken 14 December 1988, 22 days before hatching. Figure 9. Three juveniles in aquarium III about a month after hatching. Figure 10. Mantle tissue of a juvenile *N. belauensis*. Control, stained with pre-immune serum. 10% buffered formalin fixation. The mantle edge has three folds: the outer (O), middle (M), and inner (I) fold. The outer (OE) and inner (IE) epithelium cover the middle connective tissue (CT). Bar = 500 μ m. Figure 11. Similar section as Figure 10, but stained with anti-soluble matrix antiserum and PAP. Immunoreactive regions are stained red. Arrow indicates the border between the strongly stained tall mantle epithelial cells and very little-stained outer mantle fold. 10% buffered formalin fixation. Same scale as Figure 10. Figure 12. Control section of outer mantle epithelium at higher magnification. Zamboni fixation, and Hematoxylin-Eosin staining. Bar = 50 μ m. Figure 13. Outer mantle epithelium stained with anti-soluble matrix antiserum and PAP and photographed at a high magnification. Immunoreactive regions are stained red. Elongated purple structures are nuclei. Zamboni fixation. Same scale as Figure 12. Figure 14. Outer mantle epithelium stained with anti-insoluble matrix antiserum and PAP. Immunoreactive regions are stained red. Elongated purple structures are nuclei. Zamboni fixation. Same scale as Figure 12.



are the nepionic constriction and septal approximation which mark hatching (see Arnold et al., 1987; Ward, 1987; Landman et al., 1994). Those were also observed in the present study.

In agreement with previous reports (see references in Landman et al., 1983; Arnold et al., 1987; Ward, 1987), both nautilus B and C show distinct constrictions occurring at a little over $1\frac{1}{4}$ whorls from the apex. The shell diameters of 33.0 mm and 31.8 mm at the constrictions are slightly larger than the reported average of 25–30 mm (Arnold et al., 1987; Carlson, 1991; Landman et al., 1994). When an imaginary line is drawn 120° adapical of the constrictions (Davis & Mohorter, 1973; Landman et al., 1983, 1994), it intersects chamber 10 in both B and C. Accordingly, hatching must have occurred between septa 9 and 10. Similar to the finding by Landman et al. (1994), nine septa formed during embryonic development in those two animals. After hatching, nautilus B added two septa and C one septum.

The septal approximation occurs between septa 6–7 in shell B and 7–8 in shell C as reported by previous authors (Stenzel, 1964; Davis & Mohorter, 1973; Stumbur, 1975; Dauphin, 1979; Cochran et al., 1981; Landman et al., 1983, 1994). However, this approximation does not seem to coincide with the point of hatching shown above in these animals. This may indicate poor growth conditions in the aquarium prior to hatching.

Studies on stable isotope compositions of wild nautilus specimens (Eichler & Ristedt, 1966a, b; Cochran et al., 1981; Oba & Tanabe, 1983; Taylor & Ward, 1983; Crocker et al., 1985; Oba et al., 1992) show a marked shift in $\delta^{18}\text{O}$ in post-hatching septa. For example, Cochran et al. (1981) found a pronounced break in $\delta^{18}\text{O}$ from negative to positive values after the 7th septum. They also reported a significant positive correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Those results were interpreted to reflect either isotopic compositions within the egg during the embryonic stage and compositions outside environment after hatching, or outside environment throughout (Landman et al., 1994). Landman et al. (1994) have shown that in specimens of *N. belauensis* reared in temperature-controlled aquaria $\delta^{18}\text{O}$ values of both embryonic and postembryonic septa reflect the temperature of the water in which the septa formed and that $\delta^{13}\text{C}$ values probably reflect variations in the $\delta^{13}\text{C}$ of the aquarium water. The $\delta^{13}\text{C}$ could be affected by total dissolved CO_2 in the water and equilibration with atmospheric CO_2 (Landman et al., 1994). The significant positive correlation between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ found by Taylor & Ward (1983) and Cochran et al. (1981), and also by Landman et al. (1994) in the Kamoike Aquarium specimen is not shown in either nautilus B or C of our study. The $\delta^{13}\text{C}$ profiles of our study look very similar in pattern to those of *N. pompilius* studied by Cochran et al. (1981) and of the Kamoike Aquarium specimen of *N. belauensis* reported by Landman et al. (1994), but the range in our measured $\delta^{13}\text{C}$ is much higher than those authors. Crocker et al. (1985) showed that “eggwaters” of nautilus are de-

pleted in $\delta^{18}\text{O}$ relative to the ambient water. Unfortunately, we were unable to measure the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of either the fluid within the egg capsules or culture waters in this experiment. It is therefore difficult to infer accurately how the observed $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ variations in nautilus B and C are due to temperature fluctuations during the incubation period, kinetic fractionation or changes in the ambient isotopic composition of the surrounding egg-capsule fluid prior to hatching relative to seawater after hatching. However, the dramatic negative shift of $\delta^{13}\text{C}$ of the 6th (in nautilus B) and 4th (in nautilus C) septum to -4 and -5‰ could be explained if the embryos ingested portions of the egg capsules which had large negative values of $\delta^{13}\text{C}$ (-14.8‰), prior to mechanically pushing the capsule open or biting its way out of the capsule (Ward, 1987). The embryonic septa could incorporate negative carbon from the capsules and show negative changes in $\delta^{13}\text{C}$ of the carbonate septa. As reflected in the last embryonic septa No. 9, the value would increase steadily following utilization of environmental carbon, whose value should be more positive (close to 0‰). More data are needed to make any conclusion in those regards.

Similar to other molluscan shells, proteins and polysaccharides are the major components of matrix macromolecules of nautilus shells (Voss-Foucart, 1968; Weiner et al., 1977; Westbroek et al., 1979; Lowenstam et al., 1984). Low concentration of monosaccharides has also been reported in the insoluble matrix of *N. pompilius* (Tevesz et al., 1992).

By SDS gel electrophoresis Weiner et al. (1977) separated the soluble matrix proteins of *N. pompilius* shell into a minimum of six fractions. In the present study, the soluble matrix proteins of the adult shell of *N. belauensis* were found to consist of four fractions (150, 76, 66, and 50 KD). Insoluble matrix proteins of molluscan shells have not been fractionated previously by SDS gel electrophoresis except for the American oyster *Crassostrea virginica* (Kawaguchi & Watabe, 1993), and no data have been available on the nautilus insoluble matrices. Our analysis shows that 76, 66, and 48 KD proteins are the major fractions of the insoluble matrix of *N. belauensis*. The results may indicate that at least some, i.e., 76 KD or 66 KD proteins are shared by soluble and insoluble shell matrices of *N. belauensis*. Further biochemical characterization of those proteins is needed to verify the points.

In spite of the fact that the animals had been fixed post-mortem, overall structures of the mantle tissues of the juveniles were preserved relatively well. The tri-lobed mantle edge, consisting of the outer, middle, and inner fold, as well as the tall outer epithelial cells near the outer fold and their gradual decrease in height, are features similar to those of bivalve mollusks (Beedham, 1958). Tanabe et al. (1991) described a double-folded mantle in a 145-day embryo of *N. belauensis*. Their micrograph shows a small but distinct third fold below the second fold. The well-developed inner fold of the juvenile is presumably derived from the embryonic third fold.

Sites of synthesis of soluble and insoluble organic matrices of molluscan shells have not been known. By immunocytochemistry, Kawaguchi & Watabe (1993) showed in *Crassostrea virginica* that the soluble and insoluble matrices are synthesized separately, but incorporated together into mucous droplets in the mantle epithelium and secreted. However, the initial sites of the synthesis of those matrices were not elucidated. For the first time, the present results show that the soluble and insoluble matrix proteins are localized in the apical regions between the nucleus and the cell surface of the outer mantle epithelium. The mantle edge and the inner epithelium show very little immunohistochemical reaction. This observation presents clear evidence that synthesis and secretion of the nautilus shell organic matrices, both soluble and insoluble, occur in the outer mantle epithelium away from the mantle folds. The granular appearance of the reaction products may suggest that the matrix materials are within some vesicles as reported by Tsujii (1976) in bivalve mollusks. Whether or not the matrix proteins are synthesized separately and incorporated together into mucous droplets and secreted as in the American oyster (Kawaguchi & Watabe, 1993) is unknown. Further investigation is needed to clarify those points.

ACKNOWLEDGMENTS

We thank Toba Aquarium for their generous donation of adult *Nautilus belauensis*, and Mr. T. Taniguchi, Shima Marineland Foundation for his cooperation and skillful assistance in rearing the nautilus. We also thank Dr. M. Oishi, Kitasato University for antisera preparation, and Ms. J. M. Osterman and T. A. Whitaker, the University of South Carolina, for their excellent technical assistance. We are grateful to Dr. Neil H. Landman, American Museum of Natural History, and Dr. John M. Arnold, University of Hawaii for their valuable advice and critical review of the manuscript. This study was partially supported by the fund from the University of South Carolina Educational Foundation and Research Grant No. IBN9118341 from the National Science Foundation.

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Hypodermic Insemination, Oviposition, and Embryonic Development of a Pool-dwelling Ascoglossan (= Sacoglossan) Opisthobranch: *Ercolania felina* (Hutton, 1882) on New Zealand Shores

by

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Abstract. Reproductive features of the small New Zealand ascoglossan gastropod *Ercolania felina* (Hutton, 1882) were investigated in 1992 and 1993. The species inseminates by hypodermic copulation, and most individuals have mating scars and/or missing cerata. The minimum size for sexual activity (based on mating scars and egg mass production) is 3 mm long. Extensive mating damage does not reduce short-term fecundity of *E. felina*. Egg masses contain one egg per capsule; mean capsule diameter is 98 μm , and mean ovum diameter is 56 μm . Planktotrophic veliger larvae hatch 6 to 9 days after oviposition (at 13 to 16°C). The type 1 veliger shells average 119 μm long and 90 μm tall. Reproductive features of *E. felina* are generally similar to those of most of its ascoglossan counterparts on other rocky shores, although capsules and ova are slightly smaller.

INTRODUCTION

On many temperate-zone rocky shores, one or two species of ascoglossan opisthobranchs occur in intertidal pools in association with filamentous and/or siphonous green algae (Burn, 1972, 1974; Thompson, 1976; Usuki, 1977; Trowbridge, 1993a, b, 1994). Extensive information exists for the population dynamics and feeding ecology of four pool-dwelling species in the northern hemisphere: *Limapontia capitata* (Müller, 1774), *L. senestra* (Quatrefages, 1844), *Aplysiopsis enteromorphae* (Cockerell & Eliot, 1905), and *Ercolania boodleae* (Baba, 1938) (Gonor, 1961; Jensen, 1975; Thompson, 1976; Usuki, 1977; Trowbridge, 1993a, b; references therein). Furthermore, there is detailed information for reproductive features of these four species (Gascoigne, 1956; Hamatani, 1960; Greene, 1968; Baba & Hamatani, 1970; Chia, 1971; Thompson, 1976; Usuki, 1977; Trowbridge, 1993b). In contrast, comparatively less

information is available about ecological counterparts in the southern hemisphere: *Ercolania margaritae* Burn, 1974, and *Elysia australis* (Quoy & Gaimard, 1832) in Australia, *Ercolania felina* (Hutton, 1882) in New Zealand, and *Aplysiopsis sinuensis* Macnae, 1954, in South Africa.

This study focused on the New Zealand pool-dwelling ascoglossan *Ercolania felina* (formerly *Stiliger felinus*; nomenclatural change by Burn, 1974). The species was originally described by Hutton (1882a, b) with further elaborations by Eliot (1907) and Burn (1974). Key aspects of the species' biology, however, have not been investigated. I describe in this paper the mating behavior, oviposition, and embryonic development of *E. felina*. These reproductive features are important (1) in determining the population dynamics of the species and (2) in distinguishing morphologically and ecologically similar species. For example, Marcus (1973) noted that the mode of insemination was a crucial feature in distinguishing among three species of the ascoglossan genus *Bosellia* Trinchese, 1891. Gascoigne (1956, 1978) suggested that reproductive differences help distinguish between several pairs of closely related species (*Limapontia capitata* vs. *L. depressa* Alder & Han-

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cock, 1862; *Ercolania margaritae* vs. *E. boodleeae*), and that differences in copulation may be an isolating mechanism for sympatric, congeneric species.

In particular, I investigate the phenomenon of hypodermic impregnation to evaluate its ecological significance. *Ercolania felina* is a simultaneous hermaphrodite, and individuals behaving as males thrust their penial stylet through the body wall of a conspecific (Miller & Batt, 1973). Whether or not *E. felina* has a bursa to receive exogenous sperm is not known, as the internal anatomy of this species has not been fully described (but see Burn, 1974). Epidermal scars may indicate that an individual has received sperm and will deposit fertilized eggs; old individuals have scars of past sexual encounters (Miller & Batt, 1973).

Ercolania felina has been reported only from New Zealand (North and South Islands), although visually similar species occur elsewhere (see Eliot, 1907; Thompson, 1973; Burn, 1974; Jensen, 1985). *E. felina* has a maximum body length of 10 to 13 mm (Eliot, 1907; Suter, 1913; Miller & Batt, 1973; Trowbridge, 1994). It is black to chocolate brown with variable white markings that typically include the sole of the foot, tips of the cerata, anal papillae, undersides of rhinophores, and around the eyes (Eliot, 1907; Suter, 1913; Willan & Morton, 1984).

Ercolania felina occurs in high intertidal pools containing the filamentous green algae *Chaetomorpha* spp. or *Bryopsis plumosa* (Morton & Miller, 1968; Miller & Batt, 1973; Willan & Morton, 1984; Trowbridge, 1994). In the Hauraki Gulf in N.E. New Zealand, the species occurs in pools throughout the year though peak abundance is in mid to late summer (Trowbridge, 1994). Recruitment peaks in early summer, but large (presumably sexually competent) individuals are present all year; although the generation time and longevity of *E. felina* have not been explicitly investigated, the species appears to be subannual based on its seasonal recruitment and rapid growth (Trowbridge, 1994).

MATERIALS AND METHODS

Collections

Slugs used in this study were obtained from a large, shallow set of high intertidal pools at Milford Beach (longitude 174°46'30"E, latitude 36°46'25"S), just north of Auckland, in the Hauraki Gulf of the North Island of New Zealand. I made collections of *Ercolania felina* in September, October, November 1992 and May 1993.

Mating

I observed the copulatory behavior of 21 *Ercolania felina* placed together in a dish under a dissecting microscope to confirm that scars were produced by copulation. I noted whether hypodermic insemination produced visible damage and whether or not copulation was reciprocal (*sensu* Reid, 1964; Hadfield & Switzer-Dunlap, 1984). In recip-

rocal mating, ascoglossans oriented head-to-tail with their right sides adjacent; simultaneous insemination usually occurred. In non-reciprocal or unilateral mating, ascoglossans faced the same direction, and the posterior animal hypodermically inseminated its partner.

To investigate whether mating damage was size-specific, I made two separate collections of *Ercolania felina* ($n = 50$ individuals in September 1992 and $n = 64$ in October 1992) and examined them under a dissecting microscope. For the first group, I noted the extent of mating scars: none, few (1 to 10 per slug), and many (11 to > 30). Scars were light spots on the body surface and were distinct against the otherwise darkly pigmented slugs. Some of the slugs categorized as having "many scars" had large areas of pigment lost, giving animals a mottled appearance. For the second collection of slugs, I noted the presence or absence of scars and missing cerata.

For both collections, I measured *Ercolania felina* length to the nearest 0.1 mm, using an ocular micrometer, and weighed individuals to the nearest 0.1 mg on an analytical balance. Wet weight measurements of slugs can provide precise, repeatable values if animals are gently and consistently blotted on paper towels and then weighed. Although I did not test the precision of my measurements for *E. felina*, the effectiveness of this method has been demonstrated for *Placida dendritica* Alder & Hancock, 1843 (a species similar in size and mucus production to *E. felina*): average variation between repeated weighing was 2.7% (Trowbridge, 1989). Like *P. dendritica*, *E. felina* did not shed copious mucus or autotomize cerata when handled gently. I compared mean weight and length of damaged and undamaged *E. felina*. When size data were normally distributed and variances homogeneous, I used Student's *t*-tests; when the statistical assumptions were not met, I used Mann-Whitney *U*-tests.

To determine whether mating damage was related to size-specific shifts of sexual roles of *Ercolania felina*, I placed five pairs of slugs in each of three treatments: two small, two large, or one small + one large individuals per dish. I observed the slugs 12 times during the 2.5-hour experiment and noted whether they engaged in reciprocal, non-reciprocal, or no mating.

Spawning

To determine whether mating damage lowered the fecundity of *Ercolania felina*, I placed individual slugs into separate petri dishes (8.5 cm diameter × 1 cm deep) with seawater and, after 2.5 days, I weighed each egg mass produced. Wet weight measurements of egg masses can provide precise values, highly correlated to dry weight values, as demonstrated by Trowbridge (1993b) for *Aplysiopsis enteromorphae* egg masses. I compared the wet weight of egg masses produced by damaged and undamaged slugs, using a Student's *t*-test.

Because mating scars may heal, and/or slugs may self-fertilize, I investigated whether *Ercolania felina* lacking

scars would produce fertilized eggs. I measured and weighed 50 *E. felina*, noted the presence of any mating scars, and placed individual slugs into separate petri dishes with seawater. After 8 days, I noted which ascoglossans had spawned, and compared the proportion of individuals with versus without scars that produced egg masses, using a Fisher's exact test. I also calculated the cumulative frequency of spawning during the 8 days. I noted the smallest individual depositing fertilized eggs to determine the minimum size of reproduction and weighed the egg masses to determine whether short-term fecundity varied with ascoglossan size (wet weight).

In both these spawning trials, the ascoglossans were held in petri dishes with seawater but no algal food. This methodology was selected for two reasons. (1) *Ercolania felina* frequently occurs in tidepools in the absence of algal food and conspecifics (personal observation). (2) Because my questions were what the minimum size of spawning was and whether extent of mating damage affected short-term fecundity, the presence or absence of food should not have affected the results.

Embryonic Development

Using a dissecting microscope with ocular micrometer, I measured the capsule diameter of 20 fertilized eggs in each of five egg masses (< 18 hr old) and tested whether capsule size varied significantly among masses with a one-way analysis of variance (ANOVA). I also measured capsules of 10 to 20 embryos at each of the following developmental stages: gastrulae, encapsulated veligers, and recently hatched veligers. The size of uncleaved ova was estimated from a photograph taken from a compound microscope of one small, intact egg mass placed in a depression slide. From the photograph, I measured both capsule and ovum length and width ($n = 10$). Then, using the microscopic measurements of capsule diameter (previously described) and the mean percentage of capsule diameter each ovum represented (from the photograph), I calculated average ovum diameter.

To determine the developmental rates of *Ercolania felina*, for 8 days I categorized each of 29 egg masses produced in the laboratory as containing uncleaved eggs, early cleavage stages, blastulae, gastrulae, trochophores, or veligers. Ambient temperature in the room averaged 13.2°C during the September trial. I repeated the trial in May 1993 with five *E. felina* at room temperature ($\bar{x} = 15.6^\circ\text{C}$).

RESULTS

Mating

Of 21 *Ercolania felina* placed together in a dish, eight (38%) engaged in reciprocal mating, whereas the remaining 13 (62%) engaged in non-reciprocal mating within groups of two to four individuals. Mating scars were concentrated mostly over the posterior half of the body with occasional scars on cerata, rhinophores, and head. In some

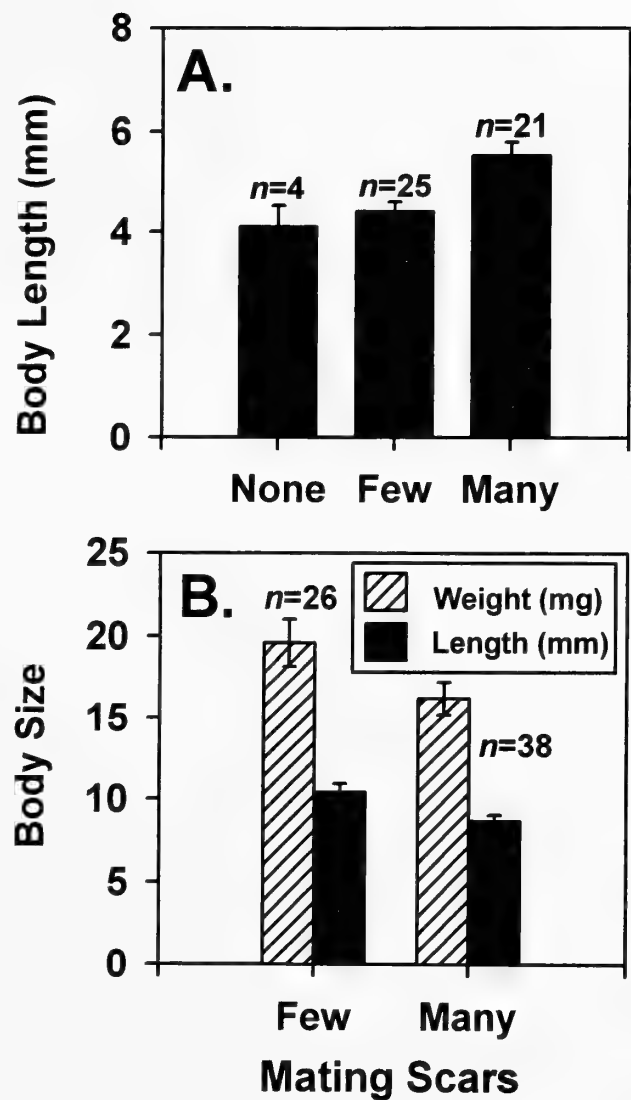


Figure 1

Size-specific damage of (A) 50 freshly collected *Ercolania felina* collected in September 1992 and (B) 64 individuals collected in October with varying degrees of mating scars on body, head, and cerata. Error bars denote ± 1 SE.

encounters, penial penetration was accompanied by the leakage of black pigment from the recipient. Cerata were lost in one encounter.

Body damage was size-specific, but the pattern differed between the two collections. In September 1992, individuals with extensive scarring (11–30+ scars/slug) and pigment loss were significantly larger than conspecifics with few (1–10 scars/slug) to no scars (Figure 1A). In contrast, in the October 1992 collection, individuals with extensive mating scars were smaller than conspecifics with few scars (Figure 1B; weight: Student's t -test, $t = 2.0$, $P = 0.052$; length: $t = 2.7$, $P = 0.009$). Furthermore, ascoglossans

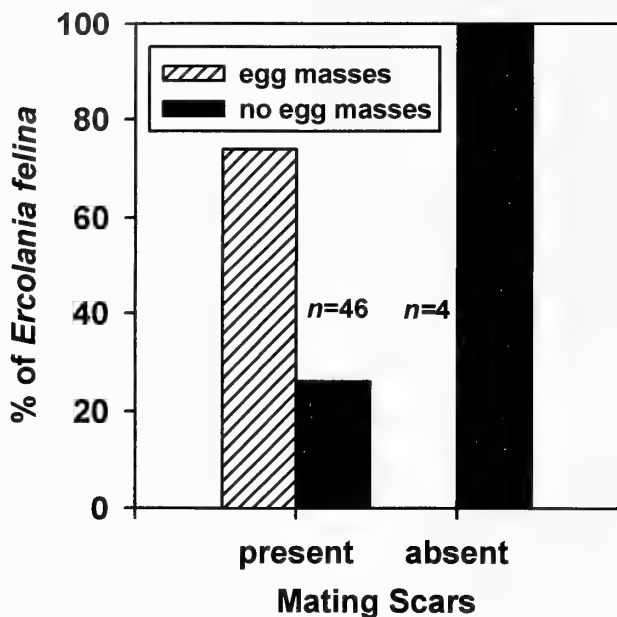


Figure 2

Proportion of *Ercolania felina* with and without mating scars that deposited egg masses in the laboratory.

with missing cerata were significantly smaller than undamaged conspecifics, on a wet weight and body length basis (Mann-Whitney U -test, $U = 293.5$, $P = 0.004$; $U = 288.5$, $P = 0.003$, respectively).

The pattern of size-specific mating damage could occur if (1) mating scars had healed and disappeared in large ascoglossans, (2) small individuals were damaged more than large conspecifics in copulation, or (3) non-mating individuals grew larger. Increased damage with increased size (Figure 1A) suggests that healing rates did not explain the pattern (in Figure 1B). Furthermore, when I placed pairs of *Ercolania felina* together (one large and one small slug), all five pairs engaged in non-reciprocal mating. However, in four of the five cases, the smaller slug attempted to inseminate larger conspecifics. Size-specific mating damage, therefore, was probably not due to large individuals acting as males.

Of 50 *Ercolania felina* collected in September 1992, only four individuals lacked mating scars. None of the unscarred individuals produced egg masses (Figure 2): these individuals apparently had not been fertilized. Twelve slugs with scars (26%) also did not deposit egg masses: thus, hypodermic insemination of sperm did not always result in fertilization of eggs in the recipient, and/or scars may persist longer than the viability of injected sperm. Significantly more *E. felina* with scars produced egg masses than conspecifics without scars (Fisher's exact test, $P = 0.008$). Furthermore, the extent of scarring did not alter the proportion of slugs that oviposited: 15 (71%) of the heavily scarred slugs and 18 (72%) of the lightly scarred individuals produced egg masses.

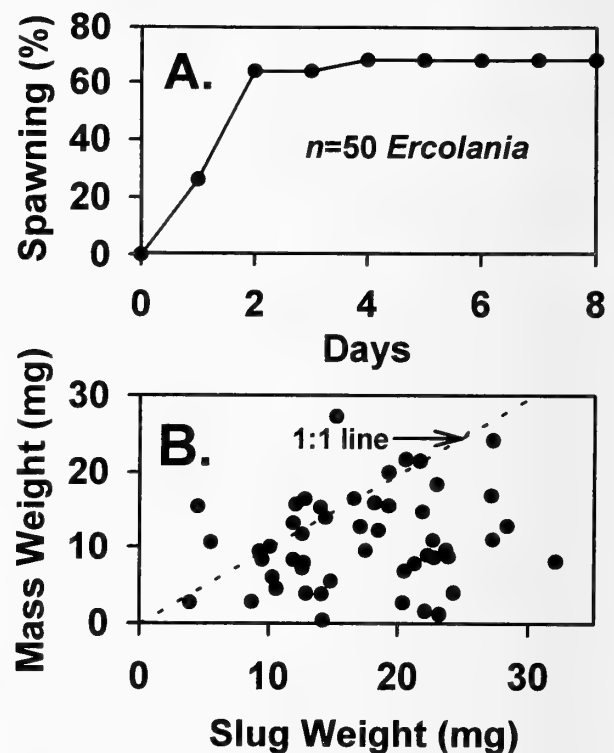


Figure 3

(A) Cumulative frequency of ovipositing (= spawning) *Ercolania felina* and (B) size-specific fecundity.

Spawning

The minimum size at reproduction of *Ercolania felina* was quite small. Of 50 specimens examined ranging from 2.7 to 7.4 mm, the smallest individual with mating scars was 2.7 mm, and the smallest individual producing an egg mass was 3.3 mm. Most individuals produced egg masses 1 to 2 days after collection from the shore or after copulation (for individuals maintained in the laboratory). Several individuals produced multiple spawn masses, but few new individuals spawned after 2 days (e.g., Figure 3A). Thus, slugs stranded in high pools with no food or conspecifics will apparently not continue to oviposit.

Egg masses weighed up to 27 mg ($\bar{x} = 10.8 \pm 0.9$ mg) and, thus, some were equal to or greater than the biomass of the slugs producing them (Figure 3B). Since slugs were weighed before oviposition, the size-specific fecundity pattern implies that the masses were hydrophilic, absorbing water after deposition. Egg mass weight did not vary significantly with ascoglossan size (body length or wet weight) or habitat (sunny vs. shady pools) (ANCOVA, $P > 0.15$ for all factors). Egg mass weight also did not vary with the extent of mating damage (Student's t -test, $t = 0.03$, $P = 0.759$, $n = 50$).

Ercolania felina produced egg masses that were typically white (a few were yellow) and contained one egg per

[illegible]

Table 2

Reproductive features of six species of pool-dwelling ascoglossan opisthobranchs. Comparable information for two other species, *Elysia australis* and *Aplysiopsis sinuensis*, is lacking.

Species	Max. body length (mm)	Hypodermic insemination	Egg diameter (μ m)	Capsule diameter (μ m)	Veliger shell	Encapsulated stage (d)	References
<i>Limapontia capitata</i>	8	yes	60–100	100	type 1	7–8	Gascoigne, 1956; Chia, 1971; Thompson, 1976
<i>Limapontia senestra</i>	6	yes	200–400	350 \times 550	—	24	Gascoigne, 1956; Chia, 1971; Thompson, 1976
<i>Aplysiopsis enteromorphae</i>	27	—	—	70–140	type 1	5–6	Greene, 1968; Trowbridge, 1993a,b, <i>personal observation</i>
<i>Ercolania boodleae</i>	15	yes	65–100	100–150	type 1	7	Hamatani, 1960; Baba & Hamatani, 1970; Usuki, 1977
<i>Ercolania margaritae</i>	14	no	80	—	—	—	Burn, 1974
<i>Ercolania felina</i>	15	yes	56	71–119	type 1	6–9	Trowbridge, <i>this study</i>

1975, 1978; Reid, 1964; Baba & Hamatani, 1970; Jensen, 1986). Hypodermic injection of sperm “randomly” over the body surface has been reported for four other species: *Alderia modesta* (Lovén, 1844); *Elysia maoria* Powell, 1937; *Elysia subornata* Verrill, 1901; and *Bosellia corinneae* Marcus, 1973 (Hand & Steinberg, 1955; Reid, 1964; Marcus, 1973; Jensen, 1986).

Gascoigne (1985), however, suggested that Reid’s (1964) observations of copulation in *Elysia maoria* may have been artifacts of stressful conditions in the laboratory and questioned the ecological importance of hypodermic insemination. Jensen (1986) observed that in copulation of *Elysia subornata* “sperm is delivered into the subepidermal tissues, forming irregular white ‘spots’ after copulation.” Jensen concluded that hypodermic transfer is the usual method of insemination in two species of *Elysia*. Furthermore, my observations of extensively damaged *Ercolania felina* freshly collected from the shore indicate that hypodermic insemination over the body surface is not an artifact, that damage is often severe, and that this is the major mode of copulation of the New Zealand species.

The fate of the injected sperm in ascoglossans is not well known (Hadfield & Switzer-Dunlap, 1984; but see Jensen, 1986). Sperm injected into the body wall and haemocoel may be phagocytosed by blood cells as described by Rivest (1984) for two species of nudibranchs. On the other hand, sperm may somehow work its way through the body to fertilize the eggs. Gascoigne (1974) suggested three potential ways in which sperm may move through the body of a recipient ascoglossan (specifically *Alderia modesta*): (1) penial style spicules may lacerate adjacent tissues, thus facilitating sperm movement and (2) prostatic fluid or (3) “sperm may liberate a hyaluronidase-like substance” that may damage adjacent tissue. Whether the penial style of *Ercolania felina* has spicules or caustic fluids is not known, but hypodermic penetration does result in fertilization of eggs (Figure 2).

The possible costs of hypodermic insemination are that (1) the injected sperm may not fertilize the partner’s eggs (donor’s cost) and (2) hypodermic penetration may render an ascoglossan more vulnerable to pathogens (recipient’s cost). Rivest (1984) noted that the former risk is minimized in species that exhibit reciprocal copulation (which increases the probability that hypodermic injections will hit the partner’s bursa). In species such as *Ercolania felina* that often exhibit non-reciprocal or unilateral copulation, the donor’s cost may be high. The cost to the recipient has been largely unexplored: differences in short-term fecundity were not found in this study, but differential mortality or susceptibility to pathogens were not investigated.

The benefits of hypodermic insemination are unclear. Perhaps it eliminates the time for precopulatory courtship: this time-minimizer strategy may be particularly relevant to species inhabiting unpredictable or transient environments such as high and mid intertidal pools. Four of the six pool-dwelling species listed in Table 2 do exhibit hypodermic copulation. If there is a fitness advantage of being male, this strategy may allow individuals to enhance their fitness by inseminating all available mates. Since the majority of individuals of *Ercolania felina* exhibit mating scars, most individuals have assumed a female role at some point. Crucial information about costs and benefits of sexual roles, however, is lacking, particularly whether (1) *E. felina* stores sperm, (2) fertilization is accomplished by sperm from the most recent insemination, (3) copulation stimulates ovulation, or (4) sexual maturation is simultaneous for male and female structures. The significance of reciprocal vs. unilateral copulation in *E. felina* also merits future experimental investigation.

Spawning

Many small ascoglossans sexually mature at a small size (Hamatani, 1960; Clark, 1975; Trowbridge, 1992, 1993b,

Table 3
Comparison of egg and capsule diameters of seven species of *Ercolania*.

Species	Egg diameter (μm)	Capsule diameter (μm)	References
<i>Ercolania coerulea</i> Trinchese, 1893	70	134 \times 123	Clark & Jensen, 1981
	—	137 \times 119	Jensen, 1985
<i>Ercolania emarginata</i> Jensen, 1985	58	124 \times 104	Jensen, 1985
<i>Ercolania felina</i> (Hutton, 1882)	56	98	Trowbridge, <i>this study</i>
<i>Ercolania funerea</i> (Costa, 1867)	59.5	—	Clark & Goetzfried, 1978
<i>Ercolania fuscata</i> (Gould, 1870)	60	115 \times 85	Clark & Jensen, 1981
	65	—	Clark, 1975
<i>Ercolania fuscovittata</i> (Lance, 1962)	66.5	—	Clark & Goetzfried, 1978
<i>Ercolania gopalai</i> (Rao, 1937)	70	175 \times (width not given)	Rao, 1937

this study). Rapid maturation probably is an adaptation for species living in transient or unpredictable environments (e.g., fluctuating physical conditions in intertidal pools or fluctuating abundances of algal food). Hydrophilic egg masses were previously reported for *Aplysiopsis enteromorphae* (Trowbridge, 1993b), a pool-dwelling counterpart of *Ercolania felina*. Although absorption of water by recently deposited egg masses may be an adaptation for high intertidal life, *Alderia modesta* inhabiting high intertidal, estuarine algal mats did not exhibit this attribute (Trowbridge, 1993b).

Mean capsule diameter of *Ercolania felina* was comparable to or slightly smaller than that of other ecologically similar species (Table 2). Capsule diameter tends not to change during embryonic development in several species of ascoglossans (Chia, 1971; Clark & Jensen, 1981; Trowbridge, *this study*). Estimated ovum diameter of *E. felina* was also comparable to or smaller than that of ecological counterparts (Table 2) and other *Ercolania* spp. (Table 3).

Opisthobranch egg size is generally indicative of developmental mode, although ascoglossan eggs tend to be smaller

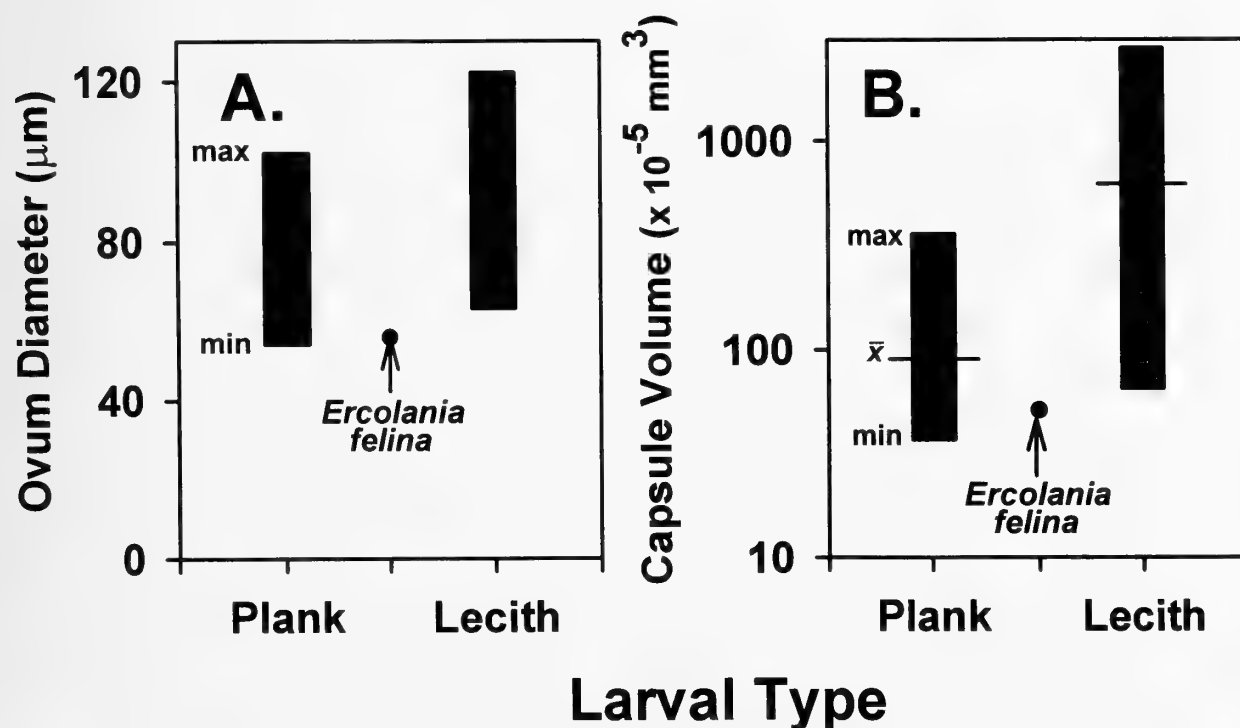


Figure 5

Ranges in (A) ovum diameter and (B) capsule volume for different species of ascoglossans with planktotrophic and lecithotrophic larvae (from Clark & Jensen, 1981) and for *Ercolania felina* (this study). Minimum, maximum, and mean (\bar{x}) values are indicated when available.

than other opisthobranch eggs (Clark & Jensen, 1981; Hadfield & Switzer-Dunlap, 1984; Hadfield & Miller, 1987). Based on results of Clark & Jensen (1981), summarized in Figure 5A, the small size of *Ercolania felina* ova indicates that the New Zealand species probably has planktotrophic larvae. No opisthobranch species reported by Hadfield & Miller (1987) with such small eggs has lecithotrophic development. Clark & Jensen (1981) suggested that capsule volume may be a better predictor of developmental mode than egg diameter for ascoglossans (see Figure 5B). *Ercolania felina* capsule volumes average $51 \times 10^{-5} \text{ mm}^3$ in volume, suggesting the species probably has planktotrophic larvae (Figure 5B).

Embryonic Development

Ascoglossan hatching times range from 5 to 33 days with an average of 11 days (25 species reviewed by Hadfield & Switzer-Dunlap, 1984). Thus, *Ercolania felina* exhibits fairly rapid embryonic development (6 to 9 days) but similar to that of other pool-swelling species (Table 2). The species' developmental rate increases slightly with warm temperature (this study) and decreases with both high and low salinity water (Trowbridge, 1994). Similar to most ascoglossans, *E. felina* produces type 1 veliger shells. The relation between veliger shell length and egg diameter of *E. felina* corresponds well with the regression line reported by Hadfield & Miller (1987) for type 1 larval shells. These results collectively suggest that the New Zealand species has reproductive features comparable to most other pool-dwelling ascoglossan species (Table 2). *Limapontia senestra*, a northeastern Atlantic species found in tidepools with the green alga *Cladophora* sp., differs however: it has large eggs and direct development (Chia, 1971; Thompson, 1976).

The fact that the reproductive ecology of the New Zealand ascoglossan *Ercolania felina* was similar to many of its northern ecological counterparts prompts questions about the conditions under which certain reproductive features occur. For example, although hypodermic insemination is reputedly uncommon in ascoglossans (Hadfield & Switzer-Dunlap, 1984), four of the six pool-dwelling species listed in Table 2 exhibit this attribute, and many others exhibiting it are intertidal species. Gascoigne (1974) also noted that warm-water ascoglossans tend to have long penial styles whereas temperate ascoglossans have short ones (for hypodermic insemination). More detailed comparative information is needed (1) about costs and benefits of hypodermic insemination and (2) environmental correlates of fecundity and developmental patterns to distinguish between taxonomic and environmental influences.

ACKNOWLEDGMENTS

Discussions with M. Miller, G. Boone, W. Ballantine, and S. Hooker improved the research. I thank R. Creese for sponsoring me at the University of Auckland, and M.

Hadfield, L. Harris, B. Roth, and two anonymous reviewers for graciously making constructive comments and suggestions on a previous draft of this paper. I thank R. Burn and W. Rudman for their comments on Australian ascoglossans, and R. Burn for his explanation of the name change of this species. The research was supported by the Leigh Marine Laboratory, University of Auckland, and National Science Foundation grant (INT-9202846) to the author. I thank L. Weber for providing me desk space in his laboratory at the Hatfield Marine Science Center, and both J. Webster and S. Gilmont for their valuable library assistance during the completion of this paper.

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Spermatogenesis and Sperm Structure in the Neotropical Pulmonate Snail *Scutalus tupaia* (d'Orbigny)

by

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Abstract. The spermatogenesis and sperm ultrastructure of *Scutalus tupaia* (d'Orbigny), a stylommatophoran pulmonate belonging to the family Bulimulidae, have been examined. The mitochondrial structure is a good indicator of the early spermatogenic stages. During spermiogenesis, three developmental stages have been distinguished on the basis of nuclear morphology and cytoplasmic changes. Different patterns of nuclear chromatin condensation were observed during spermatid differentiation: first granular, then fibers, later lamellae, finally becoming homogeneously condensed. The *S. tupaia* spermatozoon exhibits the characteristic features of euthyneuran gastropod sperm (acrosome composed of an apical vesicle and acrosomal pedestal; helically keeled nucleus with posterior invagination; midpiece composed of paracrystalline and matrix material; axoneme associated with coarse fibers) and is classified as a "modified" form. Some peculiar aspects of the mature spermatozoa, present in both the hermaphroditic duct and the fertilization pouch-spermathecal complex, are: (a) the angular position of the acrosome with respect to the longitudinal axis of the nucleus, (b) the transverse fine striation present in the acrosomal pedestal, and (c) the terminal region where the axoneme is replaced by glycogenlike granules and membranous deposits.

INTRODUCTION

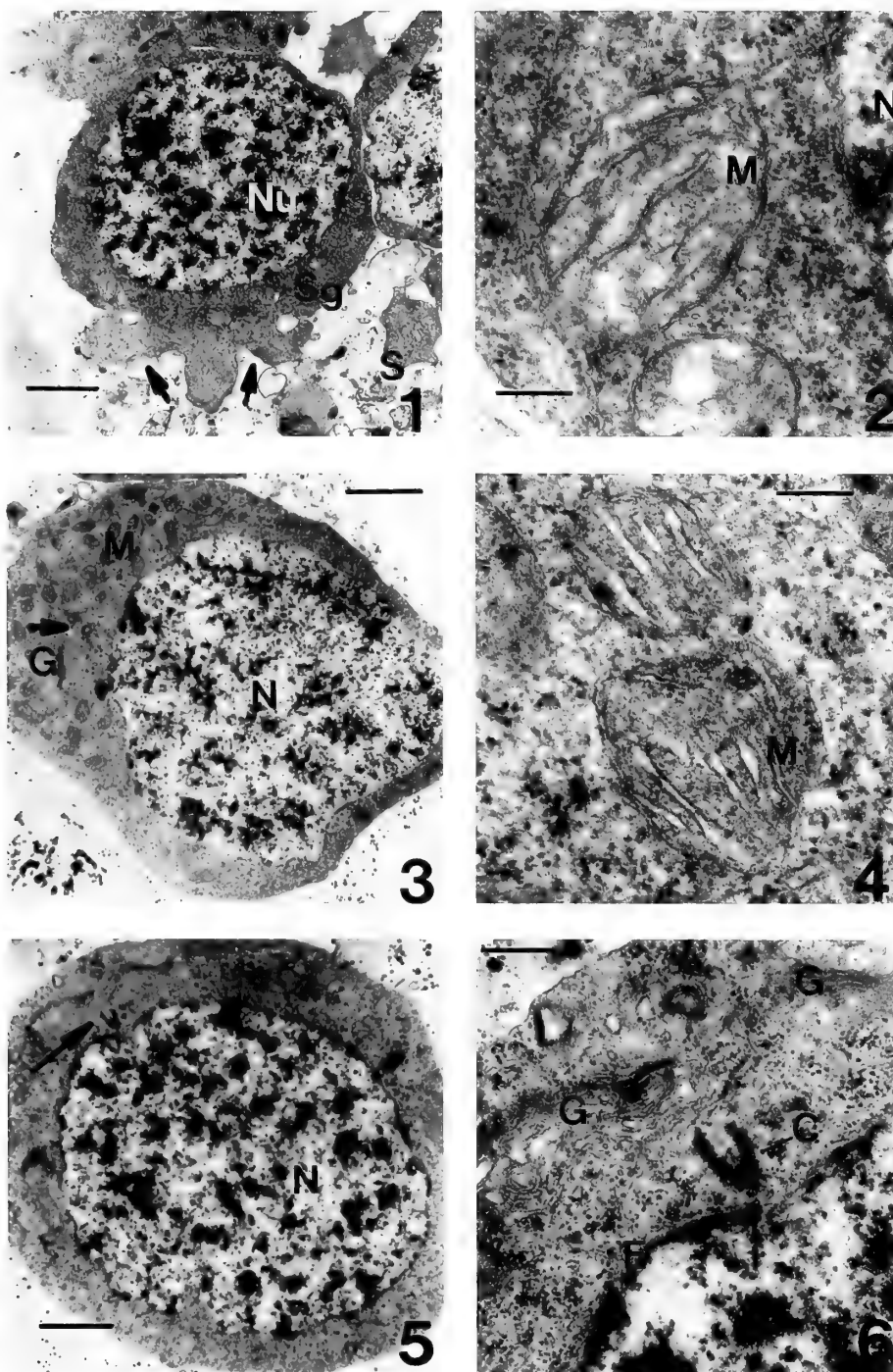
Spermatogenesis in gastropods has been studied extensively (e.g., Gatenby, 1960; Bloch & Hew, 1960; Gall, 1961; Quattrini & Lanza, 1965; Joosse & Reitz, 1969; Jong-Brink et al., 1977; Takaichi & Dan, 1977; Eckelbarger & Eyster, 1981; Medina et al., 1985, 1986; Medina et al., 1988; Griffond et al., 1991). However, little is known about this process in certain groups of pulmonate snails. Particular attention has been paid to economically important species of slugs and helicids (e.g., *Helix aspersa* Müller). The Bulimulidae form a relatively large family, mainly confined to the Neotropical region (Breure, 1979). Scarcely any information exists on the biology of the South Amer-

ican species except for systematic and zoogeographical revisions (Parodiz, 1946; Breure, 1979). Spermatozoon fine structure is useful in determining taxonomic affinity within the Mollusca (Giusti, 1971; Healy, 1988; Healy & Jamieson, 1989). Among the Gastropoda, the Prosobranchia and Basommatophora spermatozoa have been investigated extensively (e.g., Walker & Mac Gregor, 1968; Buckland-Nicks, 1973; Buckland-Nicks & Chia, 1976; Kitajima & Paraense, 1976; Healy, 1982, 1983, 1988; Buckland-Nicks et al., 1983; Azevedo & Corral, 1985; Hodgson et al., 1990; Hodgson et al., 1991; Brackenbury & Appleton, 1991). By comparison, within the Stylommatophora, relatively few ultrastructural studies have been carried out on comparative sperm ultrastructure (Anderson & Personne, 1967,

Explanation of Figures 1 to 6

Figure 1. Spermatogonia (Sg) attached to a Sertoli cell (S). Two nucleoli (Nu) are visible in the nucleus. Intercellular bridges are also distinguishable (arrows) (Scale bar = 2 μ m).

Figure 2. Mitochondrion of spermatogonium (M) showing transverse thin cristae (Scale bar = 0.3 μ m). N: nucleus Figure 3:



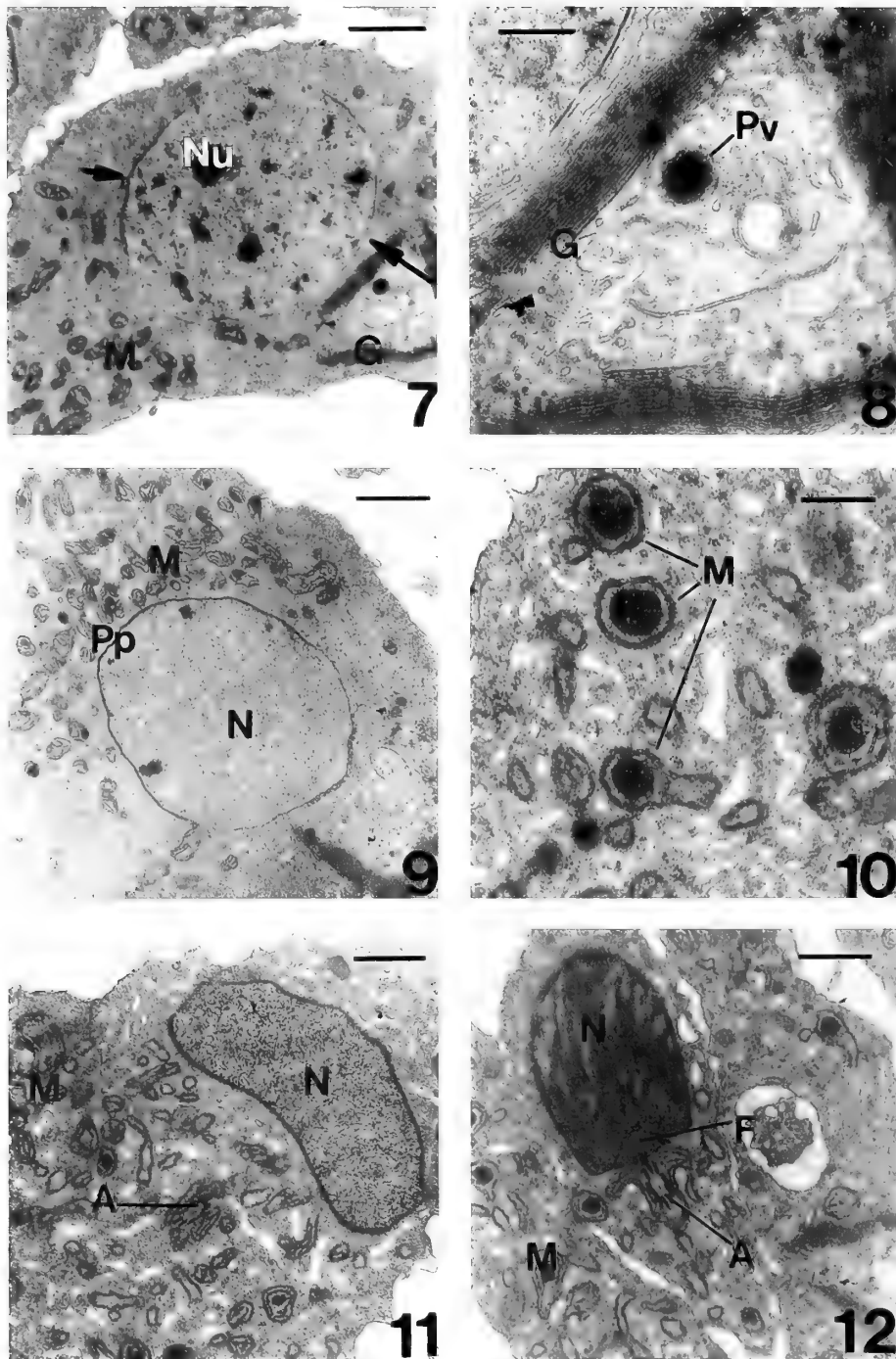
Spermatocyte I. Close to two Golgi complexes (G) a centriole (arrow) is visible. M: mitochondria (Scale bar = 3 μ m).

Figure 4. Mitochondrion of spermatocyte (M). Note the dilated intermembranous spaces of the cristae (Scale bar = 0.2 μ m).

Figure 5. Secondary spermatocyte. The centriole (arrow) is ini-

tially located under the nuclear envelope proximal to the Golgi complex (Scale bar = 1.4 μ m). N = nucleus.

Figure 6. Perinuclear region of a spermatocyte where the implantation fossa is beginning to form. A centriole (C) is in close association with the Golgi complex (G). E: nuclear envelope (Scale bar = 0.5 μ m).



Explanation of Figures 7 to 12

Figure 7. Spermatid in Stage I with nuclear plaques of the anterior (short arrow) and posterior (long arrow) sides of the nucleus. M: mitochondria, G: Golgi Complex; Nu: nucleolus (Scale bar = 1.5 μm).

Figure 8. Golgi complex (G) composed of three stacks of closely

apposed cisternae. In the central zone of the complex a proacrosomal vesicle (Pv) is formed (Scale bar = 0.6 μm).

Figure 9. Spermatid in Stage I showing a well-developed posterior plaque (Pp). M: mitochondria, N: nucleus (Scale bar = 2 μm).

1969, 1970, 1976; Bayne, 1970; Takaichi & Sawada, 1973; Healy & Jamieson, 1989; Giusti et al., 1991; Griffond et al., 1991).

The aim of the present work is to study general aspects of spermatogenesis in *Scutalus tupacii* (d'Orbigny) and to describe for the first time the spermatozoon of this species.

MATERIALS AND METHODS

Adult specimens of *Scutalus tupacii* were collected between September 1988 and March 1991 in the hillsides of the road to "Reserva Aguas Chiquitas" (El Cadillal, Tucumán, Argentina).

The ovotestis and hermaphroditic ducts were dissected out, and small pieces of them were fixed in Karnovsky's solution (Karnovsky, 1965) with 0.1 M phosphate buffer (pH 7.2) and postfixed in 2% osmium tetroxide. The tissue was rinsed several times in phosphate buffer solution, dehydrated in ethanol, and embedded in Epon-araldite. Thin sections were stained with uranyl acetate and lead citrate and viewed in a Zeiss EM 109 Electron Microscope.

RESULTS

As in other pulmonate gastropods, the ovotestis of *Scutalus tupacii* is composed of a number of acini containing germinal and non-germinal cells. The acini are blind sacs with efferent ducts that join to form the hermaphroditic duct.

In the ovotestis of adult *S. tupacii*, the acini are divided into peripheral female and central male compartments by a layer of Sertoli cells. This disposition is more evident in the bottom region of the acinus where spermiation as well as oocyte maturation takes place. Almost mature spermatozoa are released into the lumen of the acinus (male compartment). Later they are stored in the seminal vesicle (hermaphroditic duct).

Male germinal cells are attached to Sertoli cells by desmosomes. In spermatocyte and spermatid stages, associated Sertoli cells are elongated and flattened. Later they become globular while carrying late spermatids, and increase their volume before spermiation.

Spermatogonia

The spermatogonia are pear-shaped cells (9–10 μm in diameter) (Figure 1) with a round voluminous nucleus. Interphase stages are the most abundant. Usually the nucleus has a patchy appearance due to the arrangement of

the chromatin, and two or three nucleoli are usually observed. The cytoplasm has abundant free ribosomes and occasional round to oval mitochondria with a few transverse cristae (Figure 2). The rough endoplasmic reticulum is poorly developed. Generally, the spermatogonia are grouped around a Sertoli cell to which they are attached by desmosomes. At this stage, the Sertoli cells are large and irregular in shape. Intercellular cytoplasmic bridges link the group of spermatogonia.

Spermatocyte

The primary spermatocytes (Figure 3) are pear-shaped cells containing substantially more cytoplasm than the spermatogonia (15–17 μm in diameter). The round to oval nucleus usually has a nucleolus attached to the nuclear membrane. Conspicuous synaptonemal complexes are found in zygotene and pachytene stages (Figure 3). Round or elongated mitochondria with longitudinal cristae are abundant in the cytoplasm. The intermembranous spaces of the cristae are dilated, forming a clear pseudomatrix. Ribosomes are still abundant. The Golgi apparatus is well developed and located close to the nucleus surrounding the centrioles (Figure 3). Multivesicular bodies are often observed close to the dictyosomes. Primary and secondary spermatocytes are often difficult to differentiate.

Secondary spermatocytes (Figure 5) are smaller cells (7–8 μm in diameter) with a round nucleus of about 6.5 to 7 μm in diameter. In these cells the mitochondria are elongated, showing longitudinal cristae. The centriole lies close to the nuclear membrane which is beginning to invaginate to form the future implantation fossa (Figure 6).

Spermatids

Observations of nuclear and cytoplasmic organelle differentiation show that the process of spermiogenesis is divided into three stages.

Stage I: Early spermatids have a round nucleus, smaller in diameter than observed in spermatocyte II (5.5–6 μm). Nuclear chromatin has a fine granular appearance. Small nucleoli are still visible in certain early spermatids (Figure 7). The nucleus moves to the basal part of the cell and the Golgi apparatus to the apical part close to the anterior plaque. The Golgi complex is well developed with three to five stacks of closely apposed cisternae (Figure 8). Smooth endoplasmic reticulum is associated with the forming face of cisternal stacks, while the cytoplasm surrounded by

←

Figure 10. Stage II spermatid mitochondrion (M) containing dense bodies surrounded by membranes (Scale bar = 0.4 μm).

Figure 11. Spermatid in Stage II. The nucleus (N) is cup-shaped with the chromatin arranged in fine, short filaments. The mitochondria (M) begin to fuse around the axoneme, forming a thin primary layer. A: axoneme (Scale bar = 1 μm).

Figure 12. Spermatid in early Stage III. The nucleus (N) becomes elongated with chromatin arranged in thick fibers. Note the pericentriolar granular material that fills the implantation fossa (F) and contacts the mitochondrial sheath (Scale bar = 1 μm). A: axoneme.

maturing faces of the stacks exhibits several clear tubules and vesicles. In the central zone of the complex, a membrane-bound proacrosomal vesicle containing electron-dense material becomes distinguishable in this stage (Figure 8). Multivesicular bodies are frequently present. Two thickened portions of the nuclear envelope located at opposed poles are characteristic of this stage (Figure 9). These modifications, termed anterior plaque (Ap) and posterior plaque (Pp), give polarity to the cell from the beginning of the spermiogenesis and are located at the points where the acrosomal and axonemal complexes will be attached. The anterior plaque is formed by the deposition of electron-dense material on both sides of the nuclear envelope, the outside layer being thicker. The posterior plaque is more electron-dense and thicker than the anterior plaque and is formed by fine granular material deposited inside the nuclear envelope.

During spermiogenesis, great morphological modifications of the mitochondria occur as they migrate to the posterior region of the nucleus (Figure 10).

Stage II (mid-spermatids): Progressively, the nucleus changes its shape from round to ellipsoidal (Figure 11). The posterior plaque of the nuclear envelope becomes invaginated, giving rise to the implantation fossa where the basal body is attached. Granular material is located between the basal body and the nuclear envelope. In early stage II spermatids, the nuclear chromatin is condensed into short fine filaments. A great concentration of mitochondria occurs in the posterior zone of the nucleus (Figure 11). The cristae of these mitochondria are arranged concentrically around the matrix which is concentrated into an electron-dense body (Figure 10). The membranous elements of the mitochondria begin to fuse around the axoneme of the stage II spermatid midpiece forming a thin primary layer (Figure 11). Smooth endoplasmic reticulum is more abundant. The Golgi complex migrates to the posterior region of the cell.

Stage III (late spermatids): The nuclear shape of late spermatids has elongated along the antero-posterior axis, being conical to cylindrical. The chromatin becomes arranged in thick fibers which later will form lamellae (Figures 12, 13). These fibers are attached to the anterior and posterior plaques. When the nuclei are sectioned transversely in one part of the nucleus, the chromatin fibers are cut transversely, while in the opposite part, the fibers are sectioned obliquely. This suggests that the chromatin fibers are helically arranged. In transverse sections, it is possible to see the "manchette" which consists of a single row of microtubules that surround not only the nucleus (Figure 14) but also the midpiece (Figures 15, 16) of the spermatid. The microtubules are ordered at regular intervals and attached to the nuclear envelope. At the end of spermiogenesis, the "manchette" disappears.

The implantation fossa is deeper than in stage II spermatids. In late spermatids, the basal body is implanted in the basal part of the nucleus (Figure 13). The granular

material located between the basal body and the nuclear envelope is observed to contact the anterior region of the mitochondrial derivative (Figure 13). The primary mitochondrial layer has grown with the fusion of more modified mitochondria thereby forming the structurally complex mitochondrial derivative. A helical cavity runs through most of the mitochondrial derivative (Figures 13, 15). A homogeneous granular material occupies the anterior part of the helix, especially near the nucleus (Figure 13).

In transverse sections, the axoneme is surrounded by two to four rows of filaments. Two to three layers of membranous modified mitochondria enclose the axoneme plus the helical cavity (Figure 15). Some B-glycogen-like particles are seen in the intramitochondrial cavity. Later in this stage, the nuclear chromatin fibers associate, forming lamellae which become packed closely. Before spermiation, the nucleus is longer, with the chromatin homogeneously condensed, and is capped at the apex by a well-developed acrosome. The manchette is still visible. The axonemal complex consists of a 9 + 2 + 9 configuration (coarse fibers surrounding a 9 + 2 axoneme) that runs through most of the midpiece. The cytoplasm is reduced to a thin layer (Figure 13).

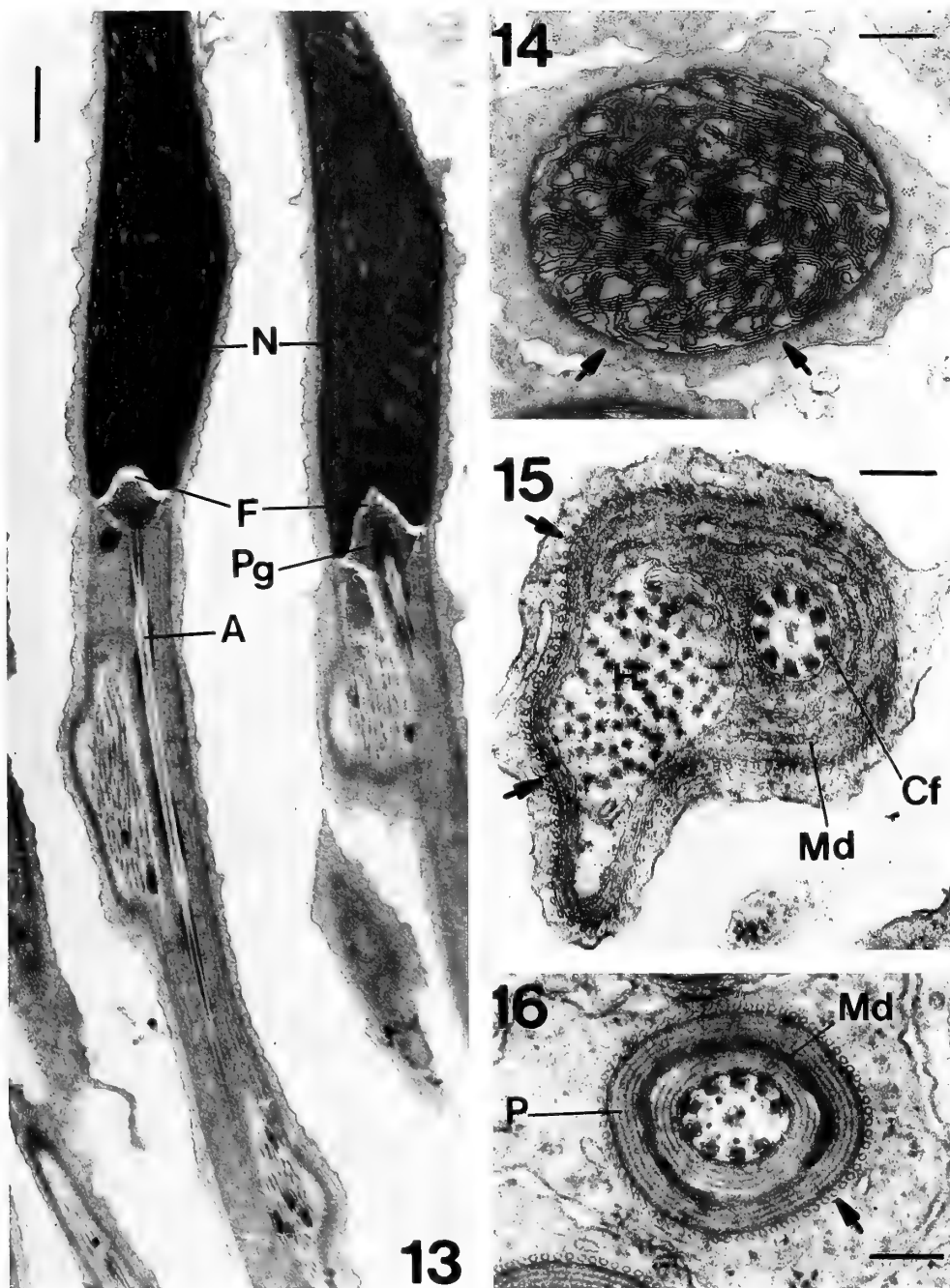
The ripe spermatid heads are embedded in the cytoplasm of the Sertoli cells in a parallel disposition close to each other. Before spermiation, the cytoplasm of the Sertoli cells extends into the lumen of the acini. These cells are abundant during spring and summer months when spermiogenesis is active. In their large cytoplasm, mitochondria are cylindrical and have transverse cristae. Most of them are located underneath the heads of the late spermatids. Abundant rosettes of glycogen are observed, as well as empty vesicles. After spermiation, ripe spermatids are released into the lumen of the acinus, and the residual cytoplasmic mass of the spermatids are phagocytosed by the Sertoli cells. Lysosomes and multivesicular bodies are frequently seen in the Sertoli cells at this stage, probably due to the destruction of the rest of the spermatid cytoplasm.

After spermiation, the Sertoli cells degenerate. In the bottom region, it is not possible to distinguish membrane boundaries, and several degenerating nuclei lie together.

Spermatozoa

The spermatozoa stored in the seminal vesicle (hermaphroditic duct) consist of an acrosomal complex and nucleus (collectively "the head" region) and midpiece (neck, glycogen helix, and terminal region).

Head: Acrosomal complex: (Figures 17, 19) The acrosome is composed of a small membrane-bound apical vesicle (0.2 μm wide, 0.3 μm long) which is a semispherical structure set on an acrosomal pedestal at the nuclear apex. The vesicle shows differentiation of internal contents, being markedly less electron-dense in the basal and peripheral areas. The pedestal (0.2 μm wide, 0.13 μm long) shows somewhat fine irregular transverse striations and a relatively electron-lucent central zone. It is positioned at the



Explanation of Figures 13 to 16

Figure 13. Longitudinal section of Stage III spermatid (Scale bar = $0.9 \mu\text{m}$). N: nucleus, F: implantation fossa, Pg: pericentriolar granules, A: axoneme.

Figure 14. Cross section of the nucleus of Stage III spermatid. Note that the nuclear chromatin is arranged in lamellae. A single row of microtubules (arrows) surrounds the nucleus (Scale bar = $0.4 \mu\text{m}$).

Figure 15. Transverse section of stage III spermatid midpiece. Three rows of filaments plus layers of mitochondrial derivative

surrounds the axoneme complex. A single helix with glycogen-like particles runs through most of the mitochondrial derivative (Scale bar = $0.2 \mu\text{m}$). Cf: coarse fibers, Md: matrix material of the mitochondrial derivative, H: helix, arrows: microtubules of the "manchette."

Figure 16. Spermatid III: A lower transverse section of the midpiece showing matrix (Md) and paracrystalline (P) components of mitochondrial derivative (Scale bar = $0.2 \mu\text{m}$). Arrow: microtubules.

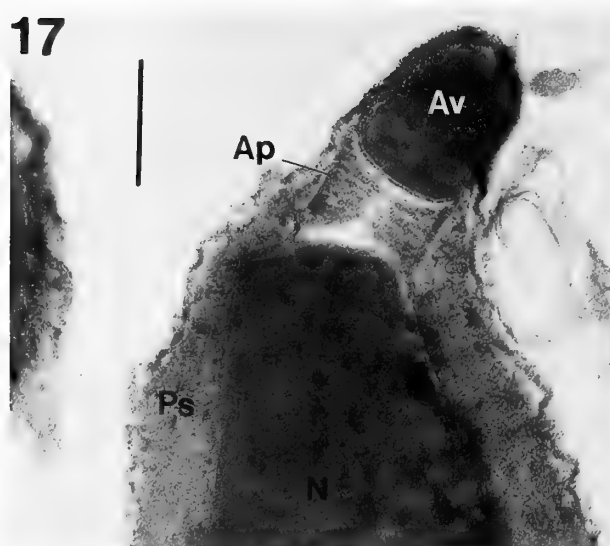


Figure 17

Acrosomal complex of a mature spermatozoon. Note the angular position of the acrosome with respect to the longitudinal axis of the nucleus. Av: acrosomal vesicle, Ap: acrosomal pedestal, N: nucleus, Ps: perinuclear sheath (Scale bar = 0.2 μ m).

extreme apex of the nucleus. A third, presumably acrosomal, component is the perinuclear sheath which is formed by granular material that surrounds the anterior half of the nucleus (Figure 20). Both the apical vesicle and the pedestal are located at an angle of about 45° with regard to the longitudinal axis of the nucleus (Figure 17).

Nucleus: The nucleus (Figures 19, 20, 21) is 7.5 μ m long and 2.3 μ m in diameter at the base, helically coiled and basally invaginated, forming an implantation fossa where the midpiece is inserted (Figure 22). The nuclear chromatin is homogeneously condensed.

Midpiece: Neck region: The neck (Figures 18, 19, 22) is the area that fixes the midpiece to the head (Anderson & Personne, 1967). The deep implantation fossa of the nucleus is filled with the basal body which is distally continued by a circular array of nine coarse fibers/9 + 2 axoneme complex that runs through the midpiece (9 + 2 + 9 con-

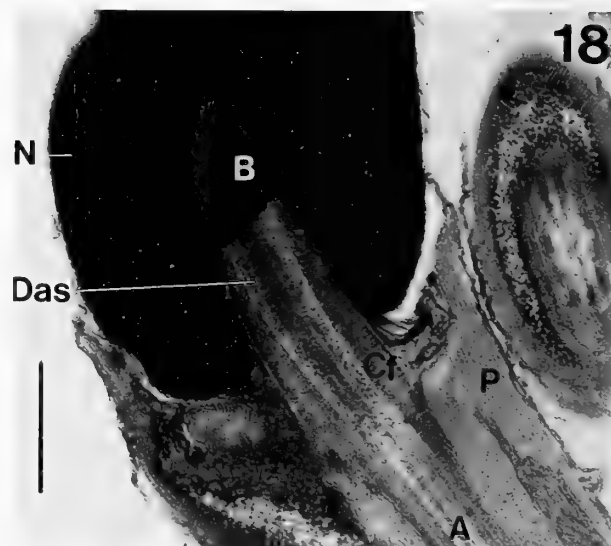


Figure 18

Longitudinal section of the neck region of a mature spermatozoon. A: axoneme, B: basal body, Cf: coarse fibers, Das: distal accessory sheath, N: nucleus, P: paracrystalline material of the mitochondrial derivative (Scale bar = 0.8 μ m).

figuration). In the neck region, the coarse fibers are thick and periodically banded. A granular distal accessory sheath (Figure 18) surrounds the central microtubules of the axoneme. The peripheral doublets of the axoneme that are embedded and masked by the coarse fibers in the neck region emerge at the beginning of the glycogen helix region. The neck region is ensheathed by the mitochondrial derivative.

Glycogen helix region: (Figures 19, 23) Along the midpiece, the axoneme and the coarse fibers are surrounded first by the external sheath of the paracrystalline component of the mitochondrial derivative. At the beginning of the glycogen helix region, the axoneme and coarse fibers are surrounded by matrix and paracrystalline materials of the mitochondrial derivative. A single helix runs through the mitochondrial derivative which is occupied from the beginning by densely packed glycogenlike granules (Figure 23). Posteriorly the layers of the matrix material of the

Explanation of Figures 19 to 25

Figure 19. Diagrammatical representation of the mature spermatozoon of *Scutalus tupacii*.

Figure 20. Cross section of the nucleus (N) showing part of the perinuclear sheath (Ps) (Scale bar = 0.3 μ m).

Figure 21. Cross section of the basal part of nucleus (N) of a spermatozoon showing the beginning of the implantation fossa (F) (Scale bar = 0.4 μ m).

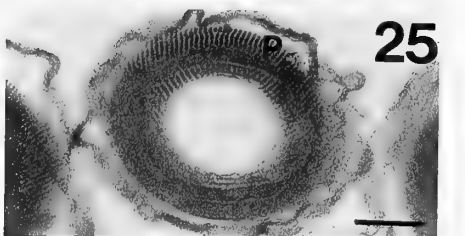
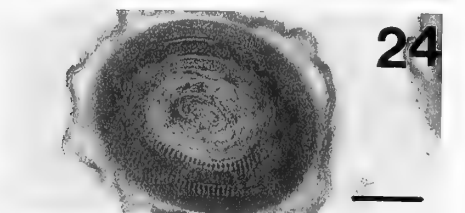
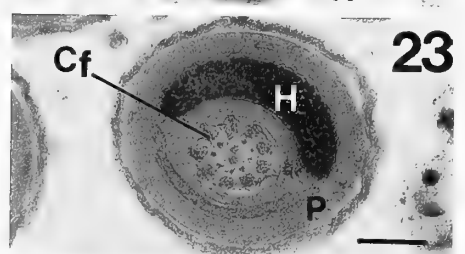
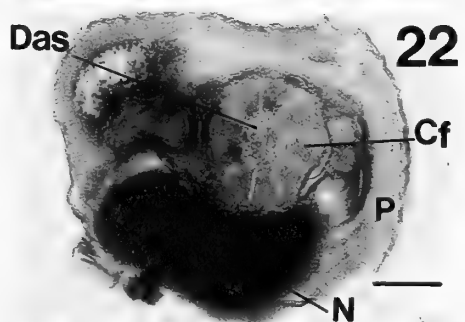
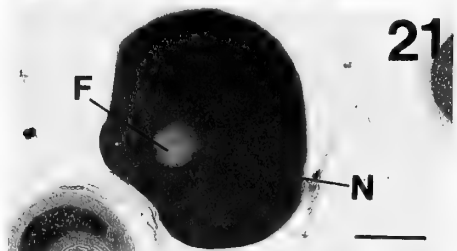
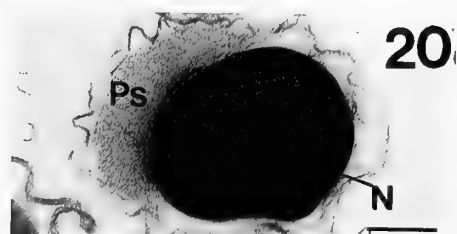
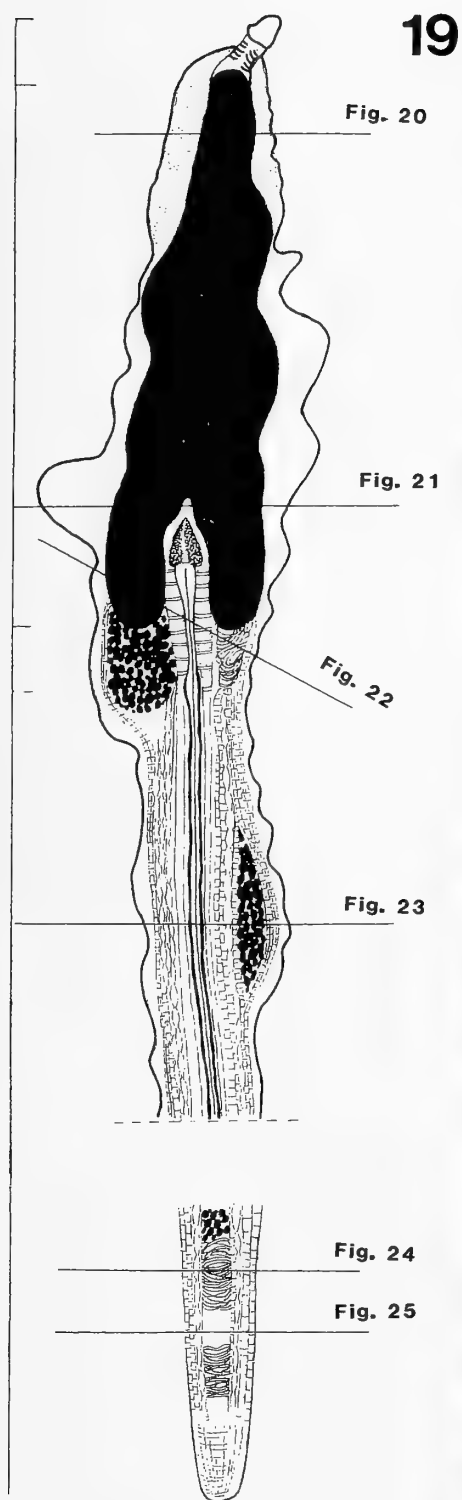
Figure 22. Transverse section of the neck region of a mature spermatozoon. Cf: coarse fibers, Das: distal accessory sheath, N:

nucleus, P: paracrystalline material of the mitochondrial derivative (Scale bar = 0.3 μ m).

Figure 23. Cross section of the helix region of a mature spermatozoon. Cf: coarse fibers, H: glycogen helix, P: paracrystalline material of the mitochondrial derivative (Scale bar = 0.7 μ m).

Figure 24. Cross section of the terminal portion of a mature spermatozoon with membranous deposits (Scale bar = 0.8 μ m).

Figure 25. Cross section of a lower part of the terminal region of the spermatozoon. P: paracrystalline material of the mitochondrial derivative (Scale bar = 0.8 μ m).



mitochondrial derivative are reduced to one layer. The glycogen helix is also reduced and eventually disappears.

Terminal region: The terminal region (Figures 19, 24, 25) of the spermatozoon begins with the loss of the axoneme which is replaced by glycogen granules and membranous deposits. The glycogen helix is absent, and a reduction in the number of matrix layers of the mitochondrial derivative was observed. The paracrystalline and a single layer of matrix component of the mitochondrial derivative continue to the tip of the spermatozoon.

Fertilization pouch-spermathecal complex: The spermathecal complex stores exogenous sperm received during copulation (Lind, 1973; Tompa, 1984; Medina et al., 1988). No ultrastructural differences between spermatozoa taken from the hermaphroditic duct and from the several tubules that conformed the spermatheca were observed. The nuclear chromatin remains homogeneously condensed, and the acrosomal complex is angularly positioned with respect to the longitudinal axis of the nucleus in the spermatozoa stored in the spermatheca.

DISCUSSION

Spermatogenesis of *Scutalus tupaia* is generally similar to that described for other gastropods (Takaichi & Dan, 1977; Jong-Brink et al., 1977; Takaichi, 1978; Dan & Takaichi, 1979; Terakado, 1981; Medina et al., 1985, 1986, 1988; Griffond et al., 1991).

Nucleoli are present in the nuclei of spermatogonia and spermatocytes, but are absent from these spermatid and spermatozoa stages. This would indicate that RNA synthesis occurs only in these early spermatogenic stages.

Free ribosomes are abundant in the spermatogonia and spermatocyte stages. The Golgi complex is present from the very beginning of spermatogenesis, but shows an increase in number of cisternal stacks and secretory vesicles from the beginning of spermiogenesis when the pro-acrosomal vesicle is formed.

Great morphological modifications of the mitochondria occur during spermatogenesis that lead to mitochondrial derivative formation. The mitochondrial derivative is paracrystalline in the spermatozoon and is characteristic of both pulmonates and opisthobranchs (Anderson & Personne, 1976), although it also occurs in other taxa (André, 1962). Most of the volume of the mitochondrial derivative is made of a proteinaceous crystal whose basic element is a globule 90 Å in diameter (Favard & André, 1970). These mitochondrial structural transformations, possibly associated with the energy requirements of the cell, allow the use of these cytoplasmic organelles as accurate indicators of the different spermatogenic stages.

Modifications in nuclear shape are similar, although not identical, to those shown in diverse gastropod species (Takaichi, 1978; Griffond, 1980; Eckelbarger & Eyster, 1981; Terakado, 1981; Healy, 1982; Dohmen, 1983; Medina et al., 1986; Healy & Jamieson, 1989; Griffond et al., 1991).

Different patterns of nuclear chromatin condensation were observed during spermatid differentiation: first granular, then fibers, later lamellae, finally becoming homogeneously condensed.

There is no general agreement as to the forces which effect nuclear shaping. Some authors have suggested that final nuclear shape is determined from within by a specific genetically controlled pattern of aggregation of DNA and protein during condensation of the chromatin (Fawcett et al., 1971). This explanation is particularly supported by the studies on spermiogenesis in groups where the "manchette" is absent (Phillips, 1974; van Deurs, 1975), whereas other cell biologists have suggested that the microtubules that surround spermatid nuclei play an active role in nuclear shaping (Terakado, 1981; Medina et al., 1986). Phillips (1970) also suggested that nuclear condensation and shaping could be the result of interrelations of nucleus, cytoplasmic organelles, and supportive cells. In *S. tupaia*, the single row of microtubules that surrounds the spermatid nuclei is present during most of the spermiogenesis, having a close association with the nuclear envelope. Therefore, the microtubules are the external force that supports and accompanies the nuclear transformation.

The *S. tupaia* spermatozoon exhibits the characteristic features of euthyneuran gastropod sperm (Healy & Jamieson, 1989) and is classified as a "modified" form, present in species with internal fertilization (Franzén, 1955, 1977; Giusti, 1971).

The most peculiar aspect of the *S. tupaia* mature spermatozoa, present in both the hermaphroditic duct (seminal vesicle) and fertilization pouch-spermathecal complex, is the position of the acrosome at an angle with respect to the longitudinal axis of the nucleus, a condition that was previously observed by Healy & Jamieson (1989) in the sperm of *Helix aspersa* Müller (angle even more exaggerated in *H. aspersa*). The acrosomal vesicle and pedestal in late spermatids are aligned in the longitudinal axis of the nucleus, but show no angulation in the ovotestis. This peculiar position of the acrosome with respect to the nucleus appears to be associated with final maturation of the sperm cell.

Another interesting characteristic of the acrosome of the *S. tupaia* spermatozoa is the transverse striation (perpendicular to the long axis of the acrosome) in the pedestal resembling to some extent the acrosomal pedestal of certain nudibranch spermatozoa (Superfamily Doridoidea) (see Healy & Willan, 1991), although probably the striations in *S. tupaia* are not as ordered. According to Medina et al., 1985, in *Hypselodoris tricolor*, the substructure of the acrosomal pedestal could provide the acrosome with greater resistance to frontal push in order to facilitate entry into the egg during fertilization. It therefore seems probable that the function of these striations would not only be to support the acrosomal vesicle.

The distal accessory sheath consists of granular material instead of a tubular structure as in other pulmonate snails previously studied.

The terminal region of the spermatozoon shows glycogen deposits at the end of the axoneme. This peculiarity was also reported for the Bradybaenidae (see Giusti et al., 1991).

With a view to analyzing the phylogenetic relationships of the Bulimulidae, comparative studies on the spermatozoon structure are required on the various genera and subfamilies before any conclusion can be established for this Stylommatophoran group.

ACKNOWLEDGMENTS

This research is part of a doctoral dissertation presented at Tucumán National University (Argentina) under the direction of Drs. Marcelo Cabada and Ernestina Teisaire to whom I would like to express my gratitude.

I am very much indebted to Dr. John Healy who kindly agreed to read the manuscript and who has made a number of useful comments.

This research was partially supported by grants from the Argentine National Council of Scientific Research (CONICET) awarded to M. O. Cabada, and Project CIUNT 1992–1993 of E. Teisaire.

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Revised Taxonomy of Some Species of the Genus *Okenia* Menke, 1830 (Mollusca: Nudibranchia) from the Atlantic Ocean, with the Description of a New Species

by

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Abstract. Information on several species in the genus *Okenia* Menke, 1830 (*O. quadricornis*, *O. mediterranea*, *O. zoobotryon*, *O. impexa*, and *O. cupella*), is presented and their taxonomic relationships are discussed. *Okenia hispanica*, a new species from the Alborán Sea, is described. New data is given on the biology and geographical distribution of the above species.

INTRODUCTION

Marcus (1957) listed the species belonging to the genus *Okenia* Menke, 1830. In the same paper, he described two new species of this genus, collected in Brazil, namely *O. impexa* and *O. evelinae*. Marcus assigned nine species in the Atlantic Ocean (including the Caribbean, the Mediterranean, and the North Sea) to the genus *Okenia*.

Since then, several new species from this geographic area have been described, namely *Okenia sapelona* Marcus & Marcus, 1967; *O. cupella* (Vogel & Schultz, 1970); *O. ascidicola* Morse, 1972, and *O. pusilla* Sordi, 1974.

A review of the current literature reveals enormous confusion regarding the taxonomy of these species, this being caused primarily by inadequate anatomical study, or by none at all.

In this paper, the taxonomic relationships of various Atlantic species of the genus *Okenia* will be explored on the basis of material collected from Cape Verde, Cuba, Spain, and Italy during several scientific trips.

SPECIES DESCRIPTIONS

Okenia quadricornis (Montagu, 1815)

(Figure 1)

Original reference: *Doris quadricornis* Montagu 1815, 11: 17, pl. IV, fig. 4.

Synonyms: *Idalla caudata* Ørsted 1844. *Idalia inaequalis*

Forbes & Hanley 1851. *Idalia aspersa* Alder & Hancock 1845. *Idalia pulchella* Alder & Hancock 1854. *Idalia modesta* Verrill, 1875. *Okenia ascidicola* Morse 1972.

Material examined: Acitrezza, Sicily Island, Italy (37°30'N, 15°10'W), 32 m depth, 7 March 1990, 1 specimen, 3.5 mm long, SICILIA-90 expedition.

Description: The body has a background color of hyaline white (Figure 1A). The dorsum has yellow spots, and these are edged with opaque white and brown in the mid-dorsal area. The lateral part of the dorsum is white and yellow, and has several brown spots. There are long spicules in the foot, which is opaque white in color. The velum bears four appendages, similar in color to the notum, and which in our specimen are very short. There are five papillae along each pallial edge. These have the same color pattern as the dorsum. There are six branchial gills, which are white with yellow and brown spots, encircling the anus.

The lateral teeth have strong denticles. The marginal teeth are hook-shaped, and lack denticles (Figure 1B). Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

Biology: *Okenia quadricornis* feeds upon the ascidians *Molgula occulta* Kupffer, 1875, in Europe (Thompson, 1988), and *Molgula manhattensis* (De Kay, 1843) in North America (Morse, 1972).

The spawn is a long gelatinous ribbon with an average

of around 15,000 white eggs (Just & Edmunds, 1985). The egg ribbon spawned by a 15 mm specimen from Denmark was 16 mm long (Just & Edmunds, 1985), and that by a 12 mm specimen from the United States was 6 mm long (Morse, 1972).

According to Thompson & Brown (1984), the greatest depth from which this species has been collected is 60 m, at Holy Island (the North Sea) by Walton in 1908.

Distribution: Since Montagu's original description of a specimen collected in Devonshire, Great Britain (Montagu, 1815), this species has been reported from the Shetland Islands (Thompson & Brown, 1984; Platts, 1985), Norway (Odhner, 1922; Thompson & Brown, 1984; Just & Edmunds, 1985; Platts, 1985), Sweden (Odhner, 1907; Just & Edmunds, 1985; Platts, 1985), Denmark (Thompson & Brown 1984; Just & Edmunds, 1985; Platts, 1985), Ireland (Platts, 1985), Great Britain (Alder & Hancock, 1845; Pruvot-Fol, 1954; Thompson & Brown, 1984; Thompson, 1988; Just & Edmunds, 1985; Platts, 1985), the French Atlantic coast (Labbé, 1931; Vayssi re, 1913; Pruvot-Fol, 1954; Bouchet & Tardy, 1976) and Portugal (Cervera et al., 1991). Also, there have been four records from North America: Verrill (1875) in New England, Verrill (1879) in New York, and Verrill (1882) and Morse (1972) in Massachusetts.

Records also exist for several localities around the Mediterranean Sea (Poizat, 1978; Schmekel & Portmann, 1982; Cattaneo-Vietti & Barletta, 1984; Cattaneo-Vietti & Thompson, 1989).

Remarks: Montagu (1815:17) described *Doris quadricornis* as follows: "Body ovate mottled brown and white; along each side an obsolete row of tubercles, somewhat dilatable, extending from the tentacula to the vent; tentacula four, long, both pairs originating from the upper part, and approximating; the anterior shortest setiform, inclining forwards; the others filiform, reflecting backwards, the same color as the body. Vent situated near the extremity of the back, surrounded with eight or nine branched appendages." However, he appears to have depicted only two velar appendages and no lateral papillae.

Alder & Hancock (1845) described *Idalia aspersa* as having the same features as *Okenia quadricornis*. However, they made a distinction between both *O. quadricornis* and *O. aspersa* because they felt that the former had only two velar appendages.

Other authors (Thompson & Brown, 1984; Cervera et al., 1991), following Alder & Hancock's idea, suggested that both *O. aspersa* and *O. quadricornis* were two different species. On the contrary, Pruvot-Fol (1954), Bouchet & Tardy (1976), and Schmekel & Portmann (1982) reached the opposite conclusion. On the basis of the external features described in the original text by Montagu (1815) and Alder & Hancock (1845), we feel that both species are identical.

A review of the literature reveals that other nominal species of *Okenia*, namely *Idalia caudata* Ørsted, 1844,

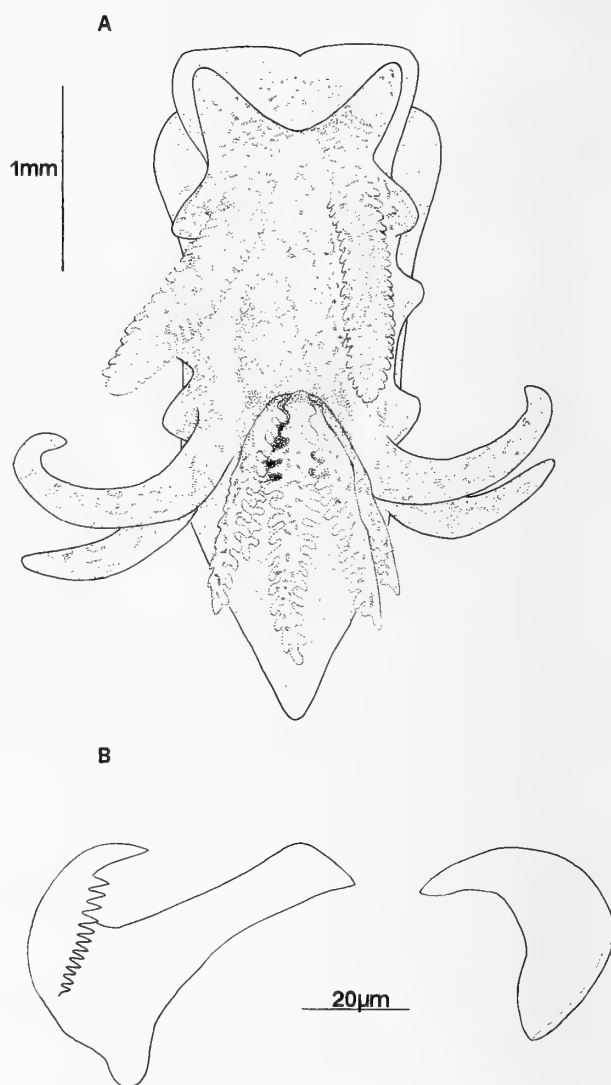


Figure 1.

Okenia quadricornis, A. dorsal view of the living animal, B. radular teeth of a half row.

Idalia inaequalis Forbes & Hanley, 1853, *Idalia modesta* Verrill, 1875 and *Okenia ascidicola* Morse, 1971 have been considered synonyms of *O. quadricornis* by the majority of authors. However, there has been some confusion surrounding the taxonomic status of *O. pulchella* Alder & Hancock, 1854. Following Lemche (1971), *O. pulchella* is a synonym of *O. aspersa* and consequently of *O. quadricornis* (see above). According to Pruvot-Fol (1954) and Thompson & Brown (1984), both *O. pulchella* and *O. aspersa* are different species, although both species possess an identical color pattern and radular tooth shape. Thompson & Brown (1984) described one specimen of *O. pulchella* whose radular teeth differed from those of *O. quadricornis*, but were identical to those of *O. elegans*. It is probable that Thomp-

Table 1

Radular formulae described for the Atlantic species of the genus *Okenia* studied in this paper.

Species	Locality	Animal length	Radular formula	References
<i>O. quadricornis</i>	England	22 mm	35x(1.1.0.1.1)	Colgan, 1914
	Massachusetts (USA)	12 mm	24x(1.1.0.1.1)	Morse, 1972
	Naples (Italy)	2 mm	24x(1.1.0.1.1)	Schmekel & Portmann, 1982
	England	10 mm	25x(1.1.0.1.1)	Thompson & Brown, 1984
	Sagres (Portugal)	8 mm	26x(1.1.0.1.1)	Cervera et al., 1991
	Sicily (Italy)	3.5 mm	22x(1.1.0.1.1)	present paper
<i>O. mediterranea</i>	Naples (Italy)	8 mm	30x(1.1.0.1.1)	Ihering, 1886
	Georgia (USA)	7.6 mm	12x(1.1.0.1.1)	Marcus & Marcus, 1967
	Naples (Italy)	5 mm	18x(1.1.0.1.1)	Schmekel, 1979
	Huelva (Spain)	8.5 mm	25x(1.1.0.1.1)	Cervera et al., 1991
	Sicily (Italy)	3 mm	13x(1.1.0.1.1)	present paper
	Tarifa (Spain)	7 mm	18x(1.1.0.1.1)	present paper
	Vigo (Spain)	15 mm	41x(1.1.0.1.1)	present paper
<i>O. zoobotryon</i>	Bermuda	5 mm	33x(1.1.0.1.1)?	Smallwood, 1910
	Bermuda	6 mm	35x(1.1.0.1.1)?	Smallwood, 1910
	Ubatuba (Brazil)	8 mm	28x(1.1.0.1.1)	Marcus, 1957
	Cuba	3 mm	17x(1.1.0.1.1)	present paper
<i>O. impexa</i>	Brazil	3 mm	17x(1.1.0.1.1)	Marcus, 1957
	Cuba	2.5 mm	18x(1.1.0.1.1)	present paper
<i>O. cupella</i>	Virginia (USA)	2 mm	10x(1.1.0.1.1)	Vogel & Schultz, 1970
	Banyuls (France)	4 mm	15x(1.1.0.1.1)	Schmekel, 1979
	Palos Cape (Spain)	3 mm	13x(1.1.0.1.1)	present paper
<i>O. hispanica</i> n. sp.	Alborán (Spain)	9 mm	20x(1.1.0.1.1)	present paper

son & Brown (1984) mistakenly studied a specimen of this latter species.

Okenia quadricornis is distinguished from other Atlantic species by the shape of its radular teeth, and externally by its smooth dorsum, which lacks papillae. *Okenia hispanica* sp. nov. (see below) is the only other species with a smooth dorsum. However, both species can be differentiated by their external coloring.

Okenia mediterranea (Ihering, 1886)

(Figures 2–3)

Original reference: *Idalia mediterranea* Ihering 1886, 8:39–46, figs. 11–13.

Synonyms: ?*Okenia sapelona* Marcus & Marcus 1967.

Material examined: Trafalgar (Fauna Ibérica I cruise), Spain (36°08'N, 6°01'W), 34 m depth, 20 July 1989, 1 specimen, 6 mm in length. Straits of Gibraltar (Fauna Ibérica I cruise), Spain (36°03'N, 5°41'W), 12 m depth, 21 July 1989, 1 specimen, 7 mm long. Acitrezza, Italy (37°30'N, 15°10'E), 35 m depth, 3 May 1990, 1 specimen, 3 mm long. Vigo, Spain (42°12'N, 9°17'W), September 1990, 7 specimens, 10 to 15 mm long. Madeira, Portugal (32°50'N, 16°17'00"W), 1993, 1 specimen.

Description: The background color of the body is white (Figure 2A). Juveniles possess a single yellow line on the

dorsum. In larger animals, up to three yellow lines, usually broken or interrupted, may occur. Generally, red spots edge these lines.

Juveniles lack tubercles on the dorsum. As the animal grows, it develops four small tubercles in the mid-dorsal area. In larger animals, several tubercles occur in the dorsum, along the three yellow lines.

The tail is white and bears a central yellow line, edged with red spots in larger animals.

There are nine branchial leaves, white with a yellow rachis, in a 15 mm-long specimen. The lamellate rhinophores are longer, and white in color. The velum bears four appendages, orange in the Mediterranean, and yellow in the Atlantic specimens. Five tentacular papillae, with the same color as the dorsum, occur along each pallial edge, the last one being bifid. The oral tentacles are long, white in color, with a yellow spot at the apex.

The reproductive system (Figure 2D) has a gametolytic gland larger than the seminal receptacle. The penis bears nine rows of hooks.

The jaw elements (Figure 2C) are short, with one to five cusps. The lateral tooth (Figure 3) bears several fine denticles. There is one cusp in the marginal tooth. Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

Biology: The prey of *O. mediterranea* consists of bryozoans such as *Alcyonidium mytili* Dalyell, 1848 (Cervera et al.,

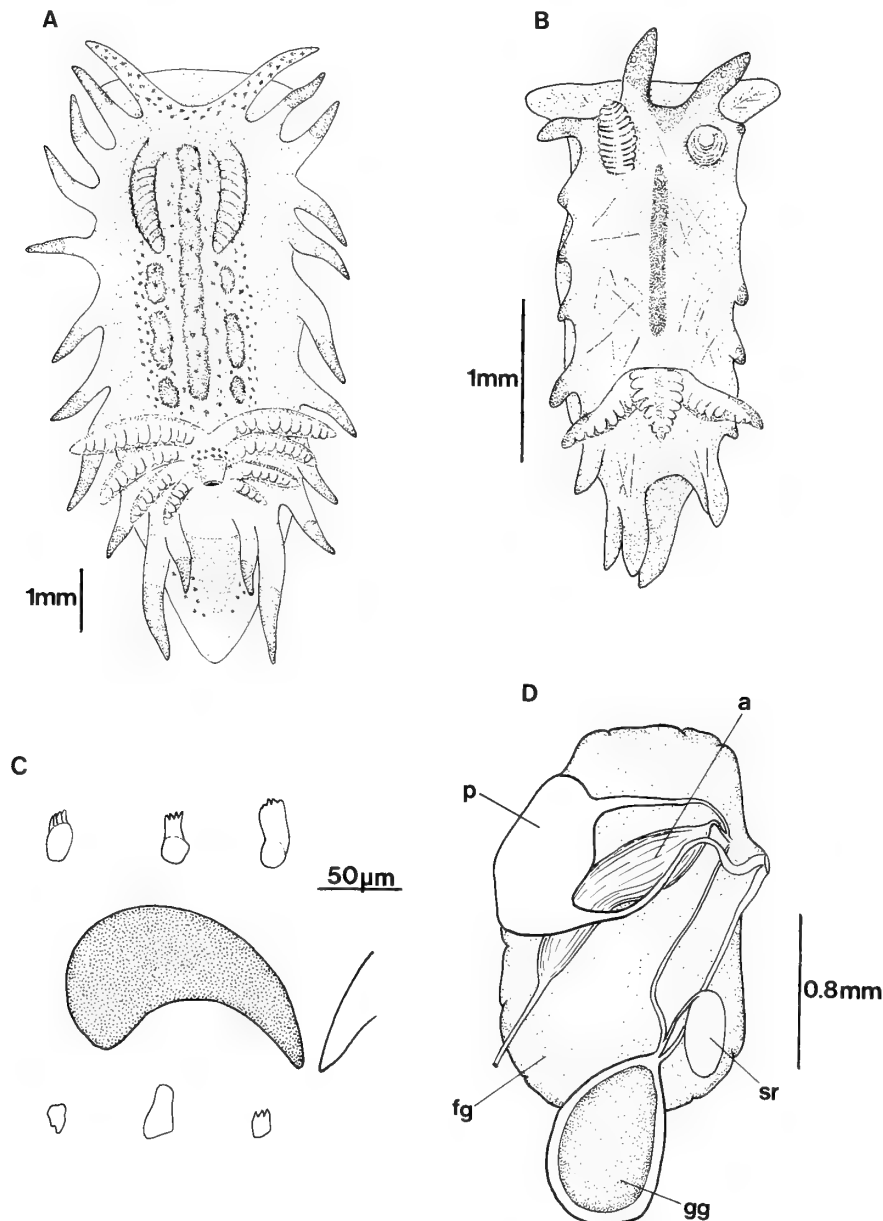


Figure 2

Okenia mediterranea, A. dorsal view of one specimen from Vigo, B. dorsal view of the juvenile specimen from Sicily, C. lateral view of the labial cuticle and detail of some elements, D. reproductive system: a, ampulla; fg, female gland; gg, gametolytic gland; p, prostate; sr, seminal receptacle.

1991). According to Cattaneo-Vietti et al. (1990), this species feeds on the octocoral *Paramuricea clavata* (Risso, 1826).

The spawn (Cervera et al., 1991) is a ribbon 10 to 12 mm long. The eggs are white in color, and their diameter is 58.5 to 78 µm.

Distribution: This species is known to inhabit Mediterranean waters (Ihering, 1886; Pruvot-Fol, 1951; Pruvot-

Fol, 1954; Schmekel, 1979; Barletta & Melone, 1976; Schmekel & Portmann, 1982; Cattaneo-Vietti & Barletta, 1984; Cattaneo-Vietti & Thompson, 1989; Cattaneo-Vietti et al., 1990).

Recently, Cervera et al. (1991) reported several specimens from Gibraltar, the first occurrence reported from the Northeastern Atlantic.

This is probably an amphiatlantic species and conspe-

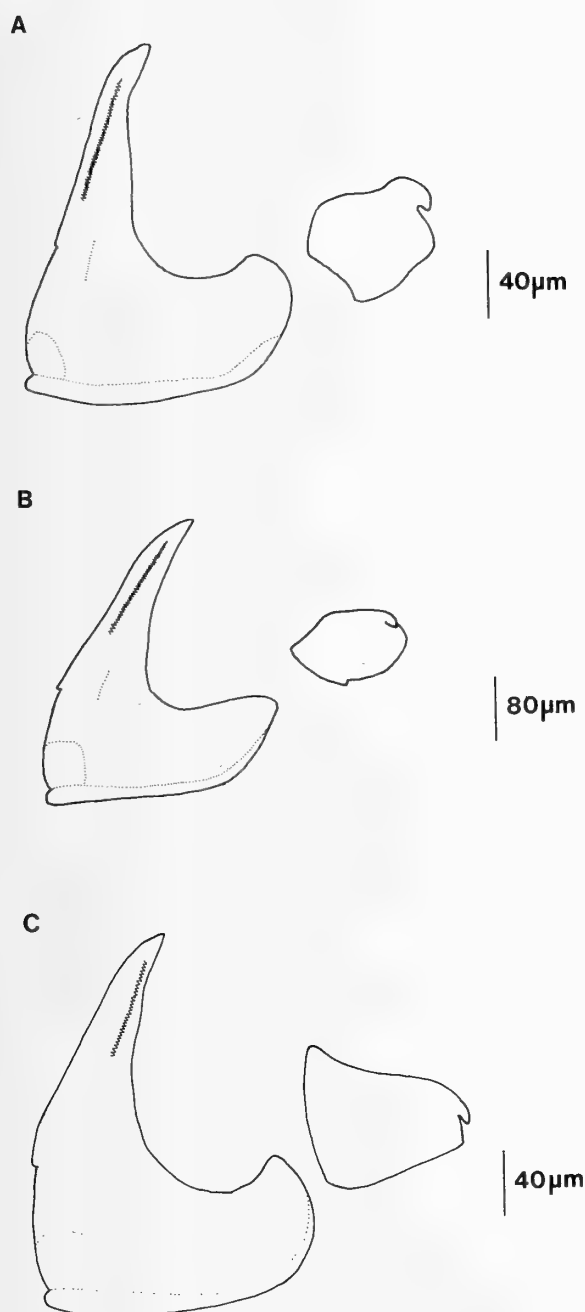


Figure 3

Okenia mediterranea, A. radular teeth of a half row of one specimen from Gibraltar Straits, B. radular teeth of a half row of one specimen from Vigo, C. radular teeth of a half row of one specimen from Sicily.

cific with *Okenia sapelona* Marcus & Marcus, 1967, described from Georgia, USA.

Remarks: Ihering (1886) defined *O. mediterranea* as: "Mantel nur am Rande mit Anhängseln, deren hinterste gespalten sind," which translates as: "The mantle only

bears papillae around its edge, the last two of which are close together." However, Ihering depicted an animal with four small tubercles on the back.

Schmekel (1979), based on Ihering's German text, suggested that *O. amoenula* (Bergh, 1907), which always has a smooth back (see below), is a synonym of *O. mediterranea*, ignoring other anatomical features which clearly differentiate both species.

On the other hand, Cervera et al. (1991) studied several specimens of *O. mediterranea* from the Iberian Peninsula and suggested that their material could belong to a different species. The confusion surrounding this species arises from the fact that as the animal grows, its external features change. The younger specimens have a smooth notum with a yellow central line. However, older specimens bear small papillae and three yellow lines on the notum.

Okenia sapelona Marcus & Marcus, 1967 described from Georgia, USA, appears to be very close to *O. mediterranea*. The radular morphology, the shape of the body, and the coloring of both species are very similar; only a bluish tone, reported in the original description of *O. sapelona* (Marcus & Marcus, 1967), distinguishes between specimens from opposite sides of the Atlantic Ocean. Nevertheless, examination of material from both Atlantic coasts is necessary before they can be confirmed as synonyms.

The color pattern of *O. mediterranea* clearly distinguishes this species from Atlantic congeners. Other species which bear small papillae on the dorsum are *O. elegans* and *O. zoobotryon*, but both species have the radular teeth shaped very differently from *O. mediterranea*.

Okenia zoobotryon (Smallwood, 1910)

(Figure 4)

Original reference: *Polycerella zoobotryon* Smallwood 1910, 143–145, fig. 10.

Synonyms: *Okenia evelinae* Marcus 1957.

Material examined: 1 specimen, Diego Pérez Key, Cuba (20°40'N, 79°25'W), 3 mm in length, 8 July 1988.

Description: The background color of the body is translucent white (Figure 4A). There are pale brown spots over the entire dorsum. The tail is similar in color to the dorsum, with opaque white spots. The oral tentacles are white with no spots. The velum bears two appendages. There are five papillae on each pallial edge. Also, there are nine papillae in the mid-dorsal area. All these papillae are shaped like chess pawns. The rhinophores are very large (Figure 4B), white in color with dark brown and opaque white spots. There are three branchial leaves in the specimen studied, pure white in color.

The lateral radular tooth (Figure 4C) has 14 strong denticles, which decrease in size toward the apex. The marginal tooth has two cusps. Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

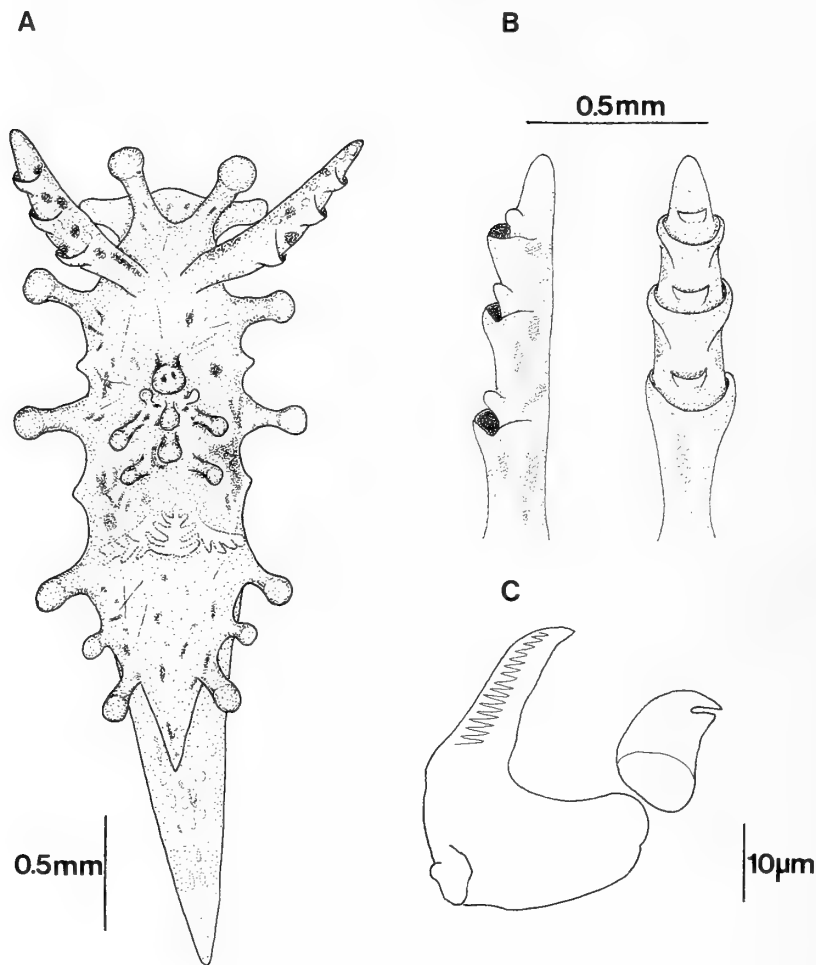


Figure 4

Okenia zoobotryon, A. dorsal view of the living animal, B. detail of the rhinophores in lateral and posterior view, C. radular teeth of a half row.

Biology: Two bryozoan species have been reported as the food of this species, *Zoobotryon verticillatum* (= *Z. pellucidum*) (Delle Chiaje, 1816) according to Smallwood (1910), and *Amathia convoluta* Lamouroux, 1841, after Marcus (1957).

The spawn is a cylindrical gelatinous mass with the number of eggs varying between 100 and 300 (Smallwood, 1910). However, Clark & Goetzfried (1978) have studied spawn masses of this species with 1200 eggs, 60.1 µm in diameter.

Distribution: This species is presently known to inhabit the western Atlantic Ocean. Type material was described from Bermuda (Smallwood, 1910), and localities recorded from Southern Brazil (Marcus, 1957, 1958), Florida, USA (Marcus & Marcus, 1960), Curaçao Island (Marcus & Marcus, 1970), Panama (Meyer, 1977), and Barbados (Edmunds & Just, 1985). Ours is the first record from Cuba.

Remarks: Smallwood (1910) described *O. zoobotryon* from Bermuda, and included it in the genus *Polycerella* Verrill, 1880, because he found a radular formula with one lateral tooth and two marginal teeth. On the basis of the odd radular formula described by Smallwood, Odhner (1941) suggested that this species should be considered the type of the new genus *Bermudella* Odhner, 1941, characterized by the radular formula $n \times (2.1.0.1.2)$.

Marcus (1957) collected several specimens of this species from Brazil, and described them as new under the name *Okenia evelinae* Marcus, 1957. This time, the radular teeth were correctly described, with a formulae $n \times (1.1.0.1.1)$. Clark (1984), with material from the type locality, re-described Smallwood's species including it in the genus *Okenia*, and considered *Okenia evelinae* a synonym of *O. zoobotryon*. Our material is identical to Clark's redescription.

The features which distinguish *O. zoobotryon* from other Atlantic species of *Okenia* include its pawn-shaped papillae and the morphology of the radular teeth. Also, the rhin-

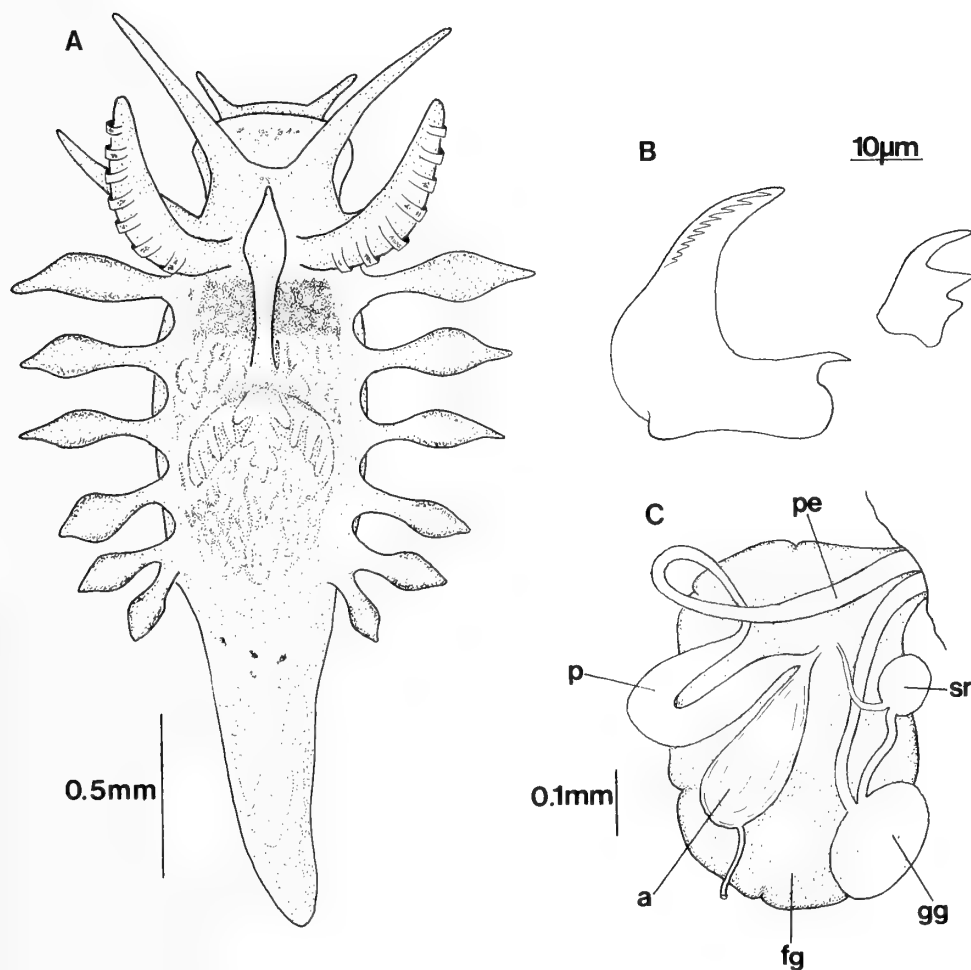


Figure 5

Okenia impexa, A. dorsal view of the living animal, B. radular teeth of a half row, C. reproductive system: a, ampulla; fg, female gland; gg, gametolytic gland; p, prostate; pe, penis; sr, seminal receptacle.

ophoral clavus lamellae of *O. zoobotryon* differ from those of other species (see Figure 4B).

Okenia impexa Marcus, 1957

(Figure 5)

Original reference: *Okenia impexa* Marcus 1957, 43:434–438, figs. 120–127.

Material examined: Flamenco Key, Cuba (20°40'N, 79°20'W), 3 m depth, 9 July 1988, 1 specimen, 2.5 mm long. Palmeira, Sal Island, Cape Verde (18°20'N, 22°30'W), 8 August 1985, 2 specimens, 1 mm long.

Description: The specimen from Cuba has a background color of hyaline white (Figure 5A), with opaque white and brown spots. There is a large dark brown patch in the middle of the notum, which bears pale spots. The specimens from Cape Verde are white in color with two

large patches on the notum. Each rhinophoral clavus has seven and five lamellae in the specimens from Cuba and Cape Verde, respectively. Four large appendages are located on the velum. The pallial edge bears six pike-shaped papillae along each side of the body, similar in color to the notum. There is a single large papillae in the middle of the notum similar in shape to the others. All the animals studied had three branchial leaves.

The reproductive system (Figure 5C) possesses a gametolytic gland twice as large as the serially arranged seminal receptacle. The prostatic portion of the vas deferens is quite short.

There are no jaws. There are 10 strong denticles on the lateral radular teeth (Figure 5B) which increase in size toward the apex. The marginal teeth bear three cusps. Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

Table 2
Characteristic features of the Atlantic species of the genus *Okenia*.

Species	Body color	Velar appendages	Dorsal papillae	Lateral papillae	Pre- sence of oral ten- tacles	Cusps of the mar- ginal teeth	Pre- sence of jaws
<i>O. quadricornis</i>	white with yellow and brown spots	four, white, yellow, and brown	none	conical, white, yellow and brown	—	1	+
<i>O. elegans</i>	rose with white and yellow spots	two or four yellow with red spots	some small papillae	conical, yellow with red spots	+	1	+
<i>O. leachi</i>	white with pink spots	four, white	some tentacular papillae	tentacular, white	—	1	+
<i>O. mediterranea</i>	white with yellow and red spots	two, yellow with red spots	some small papillae	tentacular, yellow, red and white	+	1	+
<i>O. zoobotryon</i>	white with brown spots	two, white with brown spots	some papillae, chess pawn-shaped	pawn-shaped, white with brown	+	2	—
<i>O. impexa</i>	white with brown spots	four, white with brown and yellow spots	single large papilla	pike-shaped, white with brown	+	3	—
<i>O. cupella</i>	white with brown spots	two or four white with brown spots	single large papilla	club-shaped, white with brown	+	2	—
<i>O. hispanica</i> n. sp.	white with pink and yellow spots	four, yellow and white	none	conical, yellow and white	+	1	+

Biology: The spawn of *O. impexa* is a 3 mm long mass, which contains 560 white eggs (Eyster, 1980).

Distribution: At present, *O. impexa* has been recorded from São Sebastião Island, Brazil (Marcus, 1957), North Carolina, USA (Marcus, 1961; Eyster, 1980), and Puerto Rico (Marcus & Marcus, 1970). Ours is the first record from the Eastern Atlantic Ocean.

Remarks: Anatomical features which distinguish *O. impexa* from other Atlantic species of this genus include its pike-shaped papillae and marginal radular teeth with three denticles. Our material from Cuba and Cape Verde is identical to that of the original description (Marcus, 1957).

Okenia cupella (Vogel & Schultz, 1970)

(Figure 6)

Original reference: *Cargoa cupella* Vogel & Schultz 1970, 390–393, figs. 1–5.

Synonyms: *Okenia pusilla* Sordi 1974.

Material examined: Cape Palos, Spain (36°35'N, 0°40'W), 5 m depth, 7 May 1988, 1 specimen, 3 mm in length, collected on the alga *Codium vermilara* (Oliv.) Delle Chiaje (1829) with spawn. Alborán Island, Spain (35°57'N, 3°00'W), 6 m depth, 1 specimen, 4 mm in length, collected on the bryozoan *Margaretta ceroides* Gray, 1843.

Description: The background color of the body is pale cream, with an irregular brown spotted pigmentation. There are four long appendages on the velum (Figure 6A). The pallial edge has several club-shaped papillae along each side of the body, which increase in size toward the tail. In the middle of the notum, there is a single club-shaped papillae. All these papillae are pale cream with small pale brown spots. The clavus of the rhinophores are long and yellow white in color. They bear seven cuplike lamellae projecting from the rear edge. There are four branchial gills with the same color as the body.

Eighteen small denticles occur on the lateral radular tooth, which increase in size towards the apex (Figure 6C). The marginal tooth has two blunt cusps. Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

Biology: *Okenia cupella* has been collected on the sessile phase of the scyphozoan *Chrysaora quinquecirrha* (Desor, 1851) by Vogel & Schultz (1970) and on the bryozoan *Margaretta cereoides* Gray, 1843 (present paper), which is probably its prey.

The spawn (Figure 6B) is a gelatinous bean-shaped mass with 40 white eggs in a 2 mm specimen (Vogel & Schultz, 1970), and 62 eggs in a 3 mm specimen (present paper).

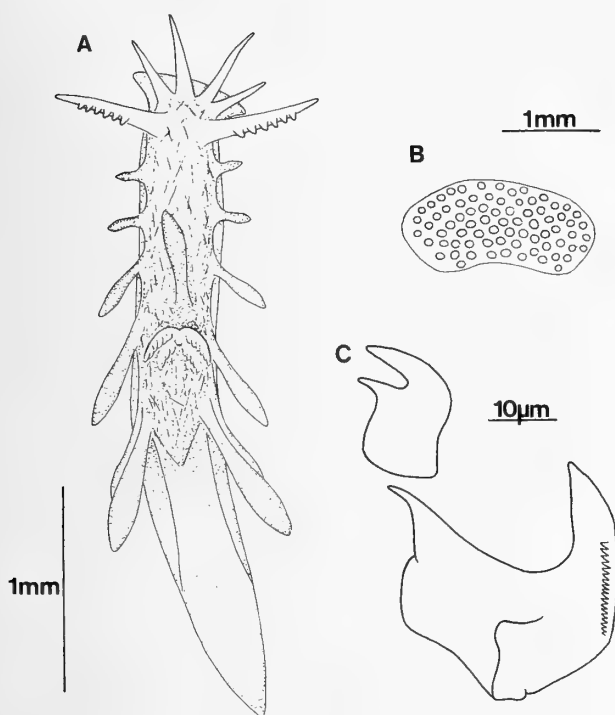


Figure 6

Okenia cupella, A. dorsal view of the living animal, B. spawn, C. radular teeth of a half row.

Distribution: *Okenia cupella* has been reported in Virginia, USA (Vogel & Schultz, 1970); Maryland, USA (Marcus, 1972); Ischia, Italy (Sordi, 1974); Naples, Italy (Schmekel, 1979); Banyuls, France (Schmekel, 1979), and Cape Palos, Spain (Templado, 1982).

Remarks: Vogel & Schultz (1970) described *O. cupella* as the type species of the new genus *Cargoa*. However, an *a posteriori* resolution of the International Commission on Zoological Nomenclature to a proposal by Burn (1971), considered *Cargoa* a synonym of *Okenia*. The only Atlantic species of the genus *Okenia* which also bears a single dorsal papilla is *O. impexa*. For this reason, Burn (1971) suggested that *O. cupella* was a junior synonym of *O. impexa* Marcus, 1957. On the contrary, Marcus (1972) believed *O. cupella* to be a valid species. We agree with Marcus' hypothesis because both species have several differences. First, the shape of the lateral papillae is different (club-shaped in *O. cupella* and pike-shaped in *O. impexa*). Also, their marginal radular teeth are different: in *O. cupella*, they have two denticles, whereas in *O. impexa* there are three. Finally, the coloration is different; *O. cupella* has small brown spots irregularly distributed on its body, whereas *O. impexa* has one or several big brown spots.

Schmekel (1979) and Templado (1982) reported specimens of *O. cupella* from the Mediterranean Sea under the name *O. impexa*, because those specimens had four velar

appendages, whereas the holotype had only two. The variability of the number of velar appendages and their increase paralleling the growth of the animal is common in other species of this genus.

On the other hand, Sordi (1974) described the species *O. pusilla* Sordi, 1974, based on a single specimen of *O. cupella*. The single specimen which was studied by this author lacks the central appendage, although the rest of its features were identical to those of *O. cupella*. The body color, radular morphology, and papillae shape described by Sordi, are identical to our material and the original description of *O. cupella*.

Okenia hispanica Valdés & Ortea, sp. nov.

(Figure 7)

Material examined: Holotype: Alborán Sea (Fauna Ibérica I cruise), Spain (39°19'N, 5°13'W), 16 July 1989, 1 specimen, 9 mm in length. Deposited in the collections of the Museo Nacional de Ciencias Naturales of Madrid (Spain), with the registration number: 15.05/17896.

Description: The background color of the body is hyaline white (Figure 7A, B). The notum possesses several pink patches. The two largest ones occur just behind each rhinophoral clavus. Also, there is a large pink patch on the anal area. The velum bears four long appendages, yellow in color, with the apex being white. The pallial edge possesses seven short papillae on each side of the body. There are five white branchial leaves with yellow tips. The short oral tentacles are white. There is a yellow line on the white tail.

The reproductive system (Figure 7E) has a spherical gametolytic gland, similar in size to the seminal receptacle. The penis bears 12 rows of hooks.

The jaw elements (Figure 7C) are long, and bear three to seven cusps. There are strong denticles on the lateral radular teeth (Figure 7D). Each marginal tooth has one cusp. Table 1 contains all the radular formulae recorded for this species. Table 2 summarizes the characteristic features of this species.

Distribution: *O. hispanica* is presently known to inhabit the Alborán Sea. This species was collected on stones at 60 m depth.

Etymology: The name of this species is derived from Hispania, the Latin name for Spain.

Remarks: *Okenia hispanica* is similar in color to *O. amoenula* Bergh, 1907, another Atlantic species with a smooth dorsum. Nevertheless, Bergh (1907) and Gosliner (1987) described specimens of *O. amoenula* as crimson and yellow in color, and MacNae (1957) as brick red and yellow, whereas in our species is pink and yellow. Internally, both species can be distinguished by the structure of the genital system and in the number of cusps in the jaws' denticles (3–7 in *O. hispanica* and 1 in *O. amoenula*). It is difficult

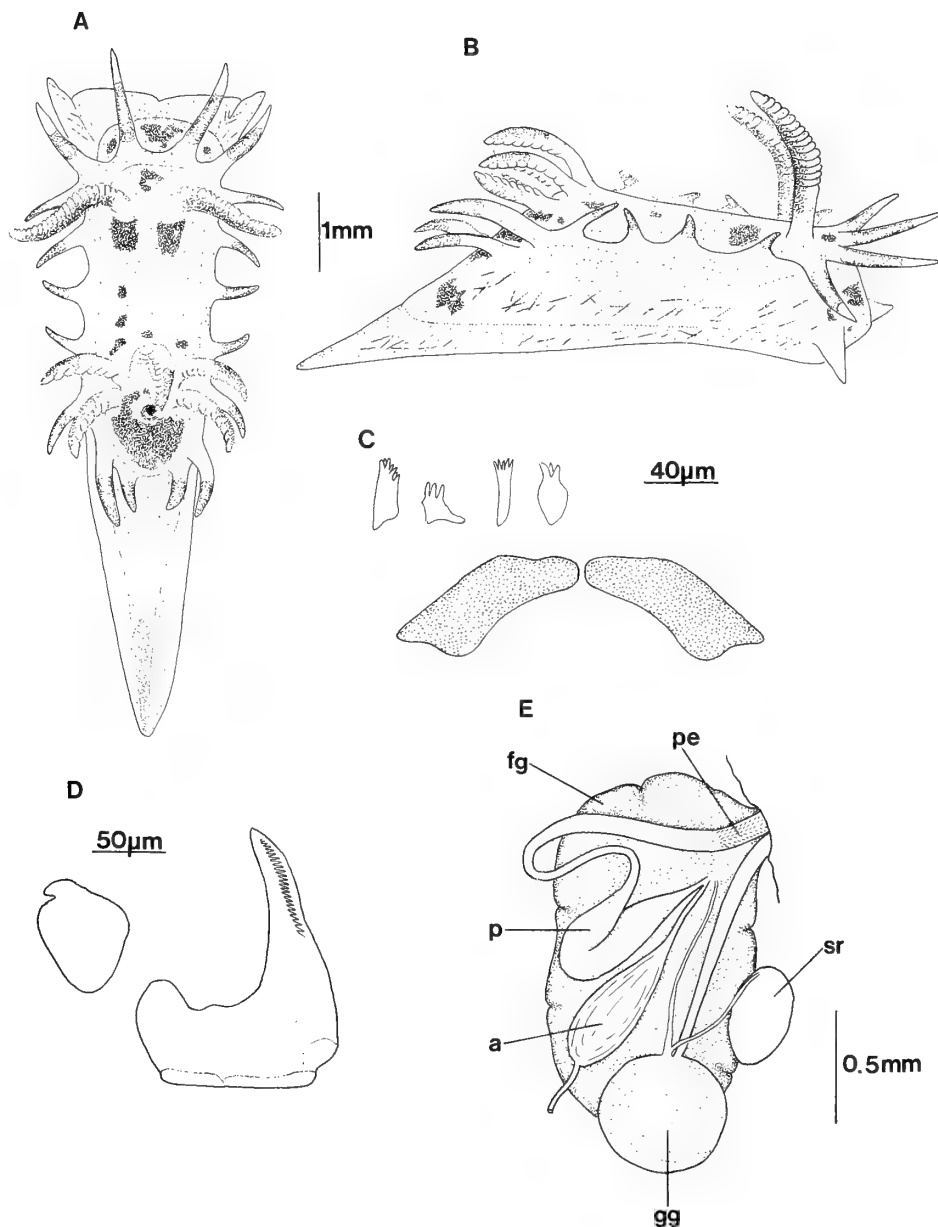


Figure 7

Okenia hispanica Valdés & Ortea, sp. nov., A. dorsal view of the living animal, B. lateral view of the living animal, C. lateral view of the labial cuticle and detail of some elements, D. radular teeth of a half row, E. reproductive system: a, ampulla; fg, female gland; gg, gametolytic gland; sr, seminal receptacle; p, prostate; pe, penis.

to separate these two species on the basis of radular morphology.

Another species that is similar to *O. hispanica* is *O. mediterranea*. Both species can be easily separated on the basis of the external features, mature *O. mediterranea* possessing at least one row of tubercles on its dorsum. The jaw anatomy of *O. hispanica* differs from that of *O. mediterranea*. The former species bears denticles with up to

seven cusps, whereas *O. mediterranea* never has more than five. Also, *O. hispanica* has 12 rows of penial hooks, whereas only nine rows occur in *O. mediterranea*.

ACKNOWLEDGMENTS

We thank Dr. Emilio Rolán (Vigo, Spain), Gonzalo Rodríguez (Universidad de Oviedo, Spain), Dr. José Templar-

do (Museo Nacional de Ciencias Naturales de Madrid, Spain), Dr. Peter Wirtz (Universidade de Madeira, Portugal), Diego Moreno (Museo Nacional de Ciencias Naturales de Madrid, Spain), and Agustín Barrajón (Málaga) for providing us with the specimens studied in this paper. We also thank Dr. Philippe Bouchet (Museum National d'Histoire Naturelle de Paris, France) for his invitation to participate in the expedition SICILIA-90, Dr. Serge Gofas (Museum National d'Histoire Naturelle de Paris, France) for his bibliographical assistance, and Eugenia Martínez (Universidad de Oviedo, Spain) for her review of the manuscript. Finally, we thank two reviewers for their constructive comments.

This paper has been supported in part by the project FAUNA IBERICA II (PB89-0081), under the auspices of the Spanish DGICYT.

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Defensive Strategies against Shell Dissolution in Bivalves Inhabiting Acidic Environments: The Case of *Geloina* (Corbiculidae) in Mangrove Swamps

by

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Abstract. The mangrove corbiculid, *Geloina erosa* has the ability to secrete periostracumlike organic sheets within the shell. The organic sheets are formed only in the portion where extensive shell dissolution has occurred. Organic sheets primarily coat the borings by microorganisms which transmit the stimulus from outer environments to mantle epithelium. They also have an important role in retarding the rate of shell dissolution. Numerous tubules are formed in the inner shell layer of the umbonal region. Each tubule contains a funnel-shaped projection of the mantle. These projections may have a sensory function, although no receptor cells have been observed. When the projection detects shell dissolution through a tubule, the epithelial cells around it may be able to secrete an organic sheet temporarily during the course of secretion of calcium carbonate. Adhesive epithelium exists on the side of each projection. Such projections may have developed primarily for adhesion to the shell. Secretion of organic sheets and secondary function of epithelial cells in *Geloina* can be interpreted as adaptations to acidic environments.

INTRODUCTION

Numerous investigations concerned with relationship between the molluscan shell form and the mode of life (or habitat) have suggested that morphological diversity of shells reflects adaptive evolution in various environments (e.g., Stanley, 1970; Seilacher, 1984).

Vermeij & Dudley (1985) pointed out that the differences in shell morphology between marine and freshwater bivalves appear to be attributable to different agents of selection in their habitats. According to them, biological agents of selection are more important in marine environments characterized by high taxonomic diversity and high bioerosion, whereas non-biological agents may be more important in freshwater environments. If the characters of molluscan shells have functional significance, certain characteristic features, which have been rarely noticed in recent studies of functional morphology, may be effective in non-marine environments where non-biological agents of selection are more important.

Acidic settings exist mostly in fresh- and brackish-water, deep-sea, and cold-sea environments, which seem to have more severe conditions for organisms with calcified shells

than ordinary warm shallow marine environments. In such environments, the taxonomic diversity of mollusks is much reduced, suggesting that non-biological agents of selection are relatively important. In acidic environments, shell dissolution may be harmful or lethal for bivalves. A large number of bivalves in such acidic environments appear to have defensive features against shell dissolution. A thick periostracum, which occurs in most bivalves living in acidic environments, appears to protect the calcified shell from dissolution. Periostracumlike organic sheets within the shell occur in several distantly related bivalve groups (Mytiloidea, Unionoidea, Solenoidea, Corbiculoidea, Myoidea) which undergo extensive shell dissolution in their environments (Oberling, 1964; Tolstikova, 1974; Lewy & Samtleben, 1979; Kat, 1985). There is a general agreement that such internal organic sheets have an important role in retarding the rate of shell dissolution under low pH conditions (Taylor et al., 1969; Tevesz & Carter, 1980; Kat, 1982, 1983, 1985).

Geloina Gray, 1842, is one of the characteristic corbiculids having internal organic sheets in their shell. *Geloina* also has several distinctive shell features, such as a heavy and thick shell and a thick periostracum. Species of this

genus live in mangrove swamps of tropical to subtropical Indo-Pacific regions in which the water has low pH, high temperature, and wide fluctuations in salinity (Morton, 1976; Isaji, 1993). Because of the acidic soil of mangrove swamps, shell dissolution of *Geloina* occurs extensively. In addition to these shell features, *Geloina* has numerous tubules locally within the inner shell layer of the umbonal region. Isaji (1993) suggested preliminarily that the tubules may be related to the formation of internal organic sheets. Although canal structure in bivalve shells has been studied (e.g., Oberling, 1955, 1964; Omori et al., 1962; Robertson & Coney, 1979; Waller, 1980), little is known about the ultrastructural features of soft tissues in the tubules.

Several shell repair experiments in bivalve shells have shown that organic sheets are secreted from the outer mantle epithelium in some bivalves (Tsujii, 1960; Beedham, 1965; Uozumi & Suzuki, 1979). While these experiments have revealed the process of shell repair in detail, it is difficult to compare these experiments and the present case, because natural shell dissolution occurs much more slowly. Therefore, little is known about the mechanism of the formation of organic sheets and the subsequent shell secretion in bivalves undergoing shell dissolution.

In this paper, I describe the properties of internal organic sheets and ultrastructural features of mantle projections within the tubules of *Geloina*. This paper also expands the possible role of tubules in the formation of organic sheets as a response to shell dissolution.

MATERIALS AND METHODS

Many specimens of *Geloina erosa* were collected from two sites in the mangrove swamp in estuaries of the Hinai River, northern Iriomote Island (24°24'N, 123°49'E; 2100 km south-east of Tokyo). The largest specimen of *Geloina erosa* collected from Iriomote Island was 125 mm in length. Judging from their large shell size, the clams seem to be long-lived. Sediment types and pH values of the surface and interstitial waters are quite different between the two collection sites. At one site, the sediment is mainly composed of sand, gravel, and fragments of marine mollusks and corals, and the pH values are relatively high (surface water: 7.23–7.79; interstitial water: 6.99–7.24). In this site, all the living specimens had undergone no shell dissolution. At the other site, the sediment is composed of muddy, fine-grained sand mixed with humus, and the pH values are relatively low (surface water: 6.99–7.13; interstitial water: 5.06–6.54). All the living specimens had undergone marked shell dissolution, especially in the umbonal region. Interestingly, they occur mainly on muddy substrata. Exact details of collection sites were described by Isaji (1993). After collection, specimens were kept alive in the experimental tank at the University of Tokyo.

Animals were fixed in 10% neutral formalin. Following dehydration, they were critical-point-dried and fractured along the umbo-ventral axis. Fractured materials were

coated with Pt for scanning electron microscopy (SEM). SEM observations were made on the critical-point-dried soft tissue removed from the shell, and also on polished and etched shells. Acetate peels were also prepared for etched shell and studied by optical microscopy. Tubule diameters (minimum diameters) were measured on the polished and fractured surfaces using SEM micrograph.

For transmission electron microscopy (TEM), animals were fixed in 2% paraformaldehyde/2% glutaraldehyde in 0.1 M cacodylate buffer (pH 7.5) for several days. Materials were subsequently washed in cacodylate buffer for 4 hours and post-fixed in 2% osmium tetroxide for 1.5 hours. Following dehydration, materials were embedded in Epon 812 resin. Ultra-thin sections were cut using an LKB-Ultratome, stained with uranyl acetate and lead citrate, and examined with a Jeol JEM-100CX TEM. One- μ m-thick sections were stained with toluidine blue for optical microscopy.

For general histological and histochemical investigations under optical microscopy, shells with periostracum and organic sheets were fixed in 10% neutral formalin and decalcified with EDTA buffered to pH 7.5 and embedded in paraffin following standard procedures. Ten- μ m-thick sections were cut and subjected to a variety of general staining and histochemical methods (Uozumi & Suzuki, 1979; López-de León & Rojkind, 1985).

RESULTS

Histological and Histochemical Reactions of Internal Organic Sheets

Organic sheets within shells are known to occur among distantly related bivalves (Kat, 1985). In the case of *Geloina*, several organic sheets (1–2 μ m thick) occur within the inner shell layer and hinge plate of specimens with marked shell dissolution (Isaji, 1993). In such specimens, organic sheets are restricted to the deeply dissolved umbonal region and just beneath the deep dissolution pit on the mid-shell region. The inner layer of highly eroded specimens consists of alternating layers of organic sheets, prismatic and/or granular structure, and complex crossed lamellar structure in order from exterior to interior. Such organic sheets, however, are not observed or are rarely observed in specimens without shell dissolution. They are light brown in color and exposed on the eroded exterior surface, suggesting high hydrophobicity. In this respect, internal organic sheets of *Geloina* are similar to the periostracum.

The complete periostracum of *Geloina* consists of three layers: outer homogeneous, middle vacuolated, and inner homogeneous ones (Figure 1). The outer layer arises along the length of the inner surface of the outer fold. The middle and inner layers arise from the tip of the outer fold. The outer and middle layers compose the external concentric folds covering the whole shell surface (Figure 1B). The periostracum is yellow to brownish in color. Its thickness attains more than 100 μ m in the marginal zone of a large

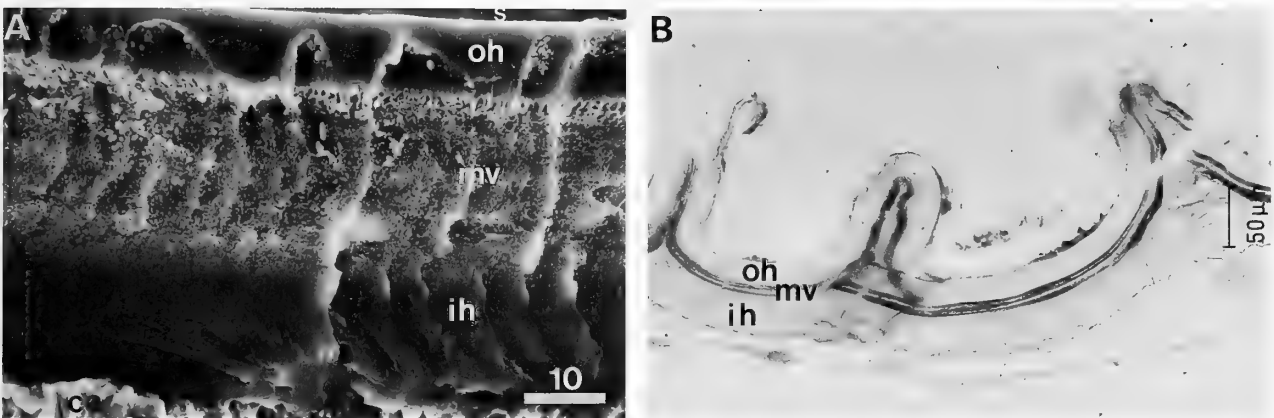


Figure 1

Periostracum of *Geloina erosa*. (A) Scanning electron micrograph of fractured section of periostracum. (B) Optical micrograph of semi-thin section (10 μ m) of periostracum. ca: calcified shell; ih: inner homogeneous layer; mv: middle vacuolated layer; oh: outer homogeneous layer; s: surface; Scale in microns.

individual. The middle layer has numerous characteristic vacuoles (Figure 1A). The boundary between the outer homogeneous and middle vacuolated layers is fairly sharp. Each vacuole situated on the outermost side of the middle layer is 1–3 μ m in diameter. The vacuole, however, gradually decreases in size toward the inner side. Therefore, the boundary between the middle and inner layers is not sharp. Similar vacuolated structure in the periostracum is also observed in *Mytilus edulis*, which also has thick periostracum (Beedham, 1958; Dunachie, 1963; Bubel, 1973).

The histological and histochemical reactions of organic sheets and periostracum are compared in Table 1. Two types of organic sheets are secreted, one situated in the umbonal region of the inner layer and one just beneath the deep pit on the mid-shell region. These two types of sheets are indistinguishable with SEM and staining reactions.

Table 1

Comparison of histological and histochemical reactions of periostracum and internal organic sheets in the shell.

	Periostracum			Organic sheet
	Outer layer	Middle layer	Inner layer	Umbo/Pit
Hematoxilin-Eosin	red	red	colorless	red
Azan-Mallory	red	red	colorless	red
Periodic acid-Schiff	+	—	—	+
Metachromasia with Toluidine blue (pH 7.0, 4.1, 2.5)	—	—	—	—
Collagen	—	—	—	—

Four staining reactions of the periostracum are the same for the outer and middle layers. Both the outer and middle layers color red with hematoxilin-eosin or Azan-Mallory stains. Both layers also exhibit no metachromasia with aqueous toluidine blue and no reaction to the collagen detective test (López-de León & Rojkind, 1985). The outer layer shows weak reaction to the periodic acid/Schiff test. However, the middle layer shows no reaction to the periodic acid/Schiff test. The inner layer does not react to any of the histological and histochemical tests examined.

The staining reactions of internal organic sheets are closely similar to those of the outer layer of the periostracum, suggesting that both layers have mucopolysaccharide.

Distribution of Tubules in the Inner Shell Layer

Numerous tubules occur locally within the inner shell layer in the umbonal region where extensive shell dissolution and internal organic sheets occur. The tubules were observed in all specimens examined regardless of the presence or absence of shell dissolution. The opening of tubules is always situated in the funnel-shaped depressions on the inner surface of the umbonal area (Figure 2A). They are concentrated in the anterior portion of the umbonal cavity, which seems to be consistent with the attached area of the inner gill (Figure 3B). In one large specimen, tubules increase in size and number toward the inner shell surface. The morphology of tubules appears to be related to degree of shell dissolution. To observe the morphology and number of tubules, the sections were controlled as in Figure 3A (a, longitudinal, b, tangential). In the specimens without marked shell dissolution in the umbonal region, the tubules are relatively small in diameter. Numerous cross sections, which are circular to elliptical in shape and rel-

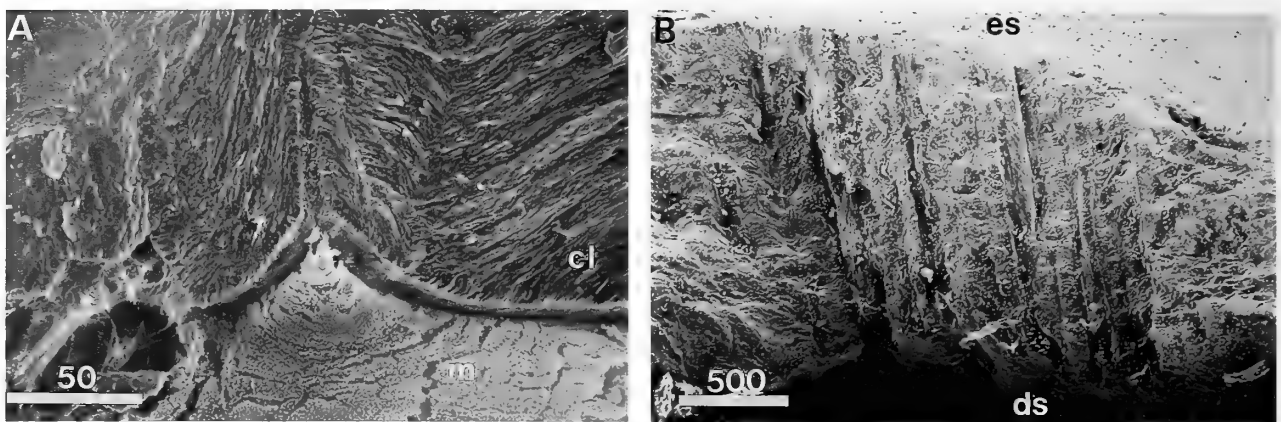


Figure 2

Scanning electron micrographs of tubules within the shell. (A) Tubule and mantle projection in the specimen without shell dissolution. (B) Tubules penetrating into the outer erosional surface in the specimen with extensive shell dissolution. cl: complex crossed lamellar layer; ds: depositional surface; es: erosional surface; m: mantle. Scale in microns.

actively short, occur in polished tangential and longitudinal surfaces (Figure 3C, D). In highly eroded specimens, cross sections of the tubules are relatively elongate and wide. The minimum diameters of large tubules measure about 100–200 μm , and more large tubules are also present. Therefore, continuous traces of each tubule are observed in tangential and longitudinal surfaces (Figure 3E, F). In

such polished surfaces, organic sheets are always observed to pass via a concave surface into a tubule, suggesting that the inner topography of the shell was formed as the organic sheets were deposited.

Some tubules in highly eroded specimens penetrate the eroded surface (Figure 2B). This results from deep shell dissolution of the umbonal region. The inner surface of

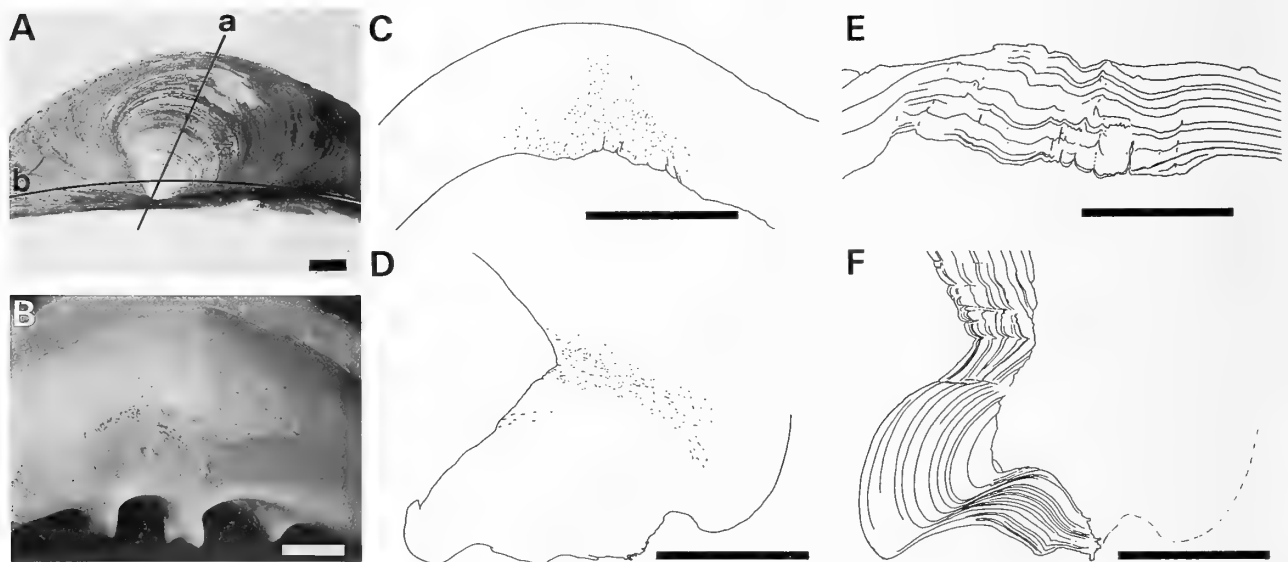


Figure 3

Tubules and organic sheets within the shell. (A) The diagram showing the direction of cutting section. a: longitudinal section; b: tangential section. (B) Distribution of tubules in the inner shell surface of umbonal region. (C) Tangential section of the specimen without shell dissolution. (D) Longitudinal section of the specimen without shell dissolution; note no internal organic sheets in (C, D). (E) Tangential section of the specimen with extensive shell dissolution. (F) Longitudinal section of the specimen with extensive shell dissolution; note numerous internal organic sheets in (E, F). Scale bar = 0.5 cm.

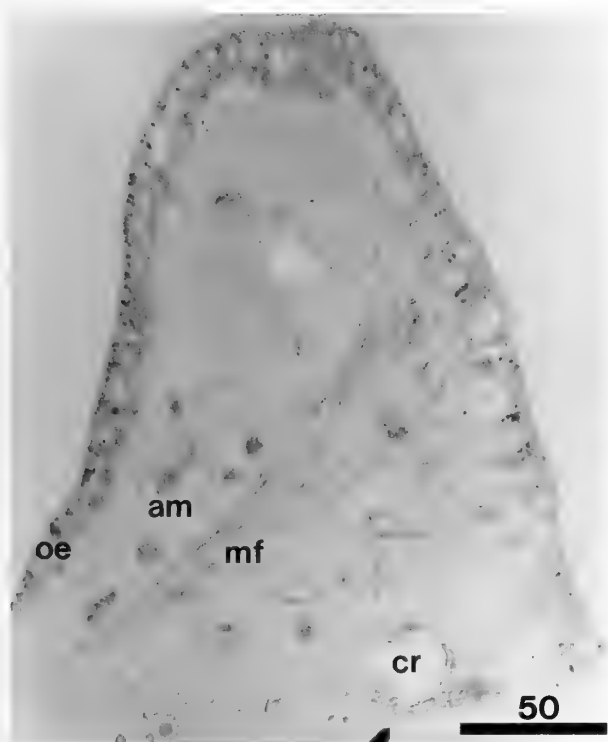


Figure 4

Optical micrographs of mantle projection in tubules. am: amoebocytes; cr: crystalline spherule; mf: muscle fibers; oe: outer epithelium. Scale in microns.

each tubule is covered with a thin prismatic shell wall (about $5\text{ }\mu\text{m}$ thick) regardless of the presence or absence of shell dissolution. It is therefore apparent that the tubules have not been expanded by dissolution as the result of penetration to the outer eroded surface. It is probable that expansion of the tubules is due to the enlargement of soft tissue existing in the tubules as described below.

Mantle Epithelium

Each tubule contains a funnel-shaped projection of mantle tissue (Figure 2A, 4). The base of a projection is conical, corresponding to the depression on the inner surface of the shell. Only the outer layer of the mantle is inserted into the funnel-shaped opening of the tubule. The projection of the mantle has a multicellular composition of the outer epithelium. The projection varies in size corresponding to the diameter of tubules. In some cases, the projection protrudes up to $200\text{ }\mu\text{m}$ in height, but is never stretched out to the entire length of the tubule.

With transmission electron microscopy, three types of epithelial cells can be distinguished in the umbonal region on the basis of cytological criteria. Epithelium at the tip of the projection appears to consist of simple columnar cells with a basally situated nucleus (Figure 5A). The cells

measure about $20\text{ }\mu\text{m}$ in height and about $10\text{ }\mu\text{m}$ in width. The cytoplasm appears granular rather than homogeneous. Organelles such as mitochondria and electron-dense secretory granules of different sizes are observed, but no Golgi bodies and endoplasmic reticula are observed in this specimen. Numerous microvilli are observed on the outer surface of the epithelium. A few bundles of fibrils are also observed.

Epithelium at the general mantle surface in the umbonal region appears to consist of simple cuboidal cells (Figure 5B). Each epithelial cell in this region measures about $10\text{ }\mu\text{m}$ in height and less than $10\text{ }\mu\text{m}$ in width. No apparent difference is observed besides their shape and size in comparison with the epithelium situated on the tip of the projections.

Epithelial cells at the lateral side of a projection have numerous bundles of fibrils showing high electron-density (Figure 5C-E). At the apical end of the cell, the surface is covered by very short microvilli. The bundles of fibrils spread out near the outer surface so as to send a small bundle to each microvillus. The tips of microvilli bear hemidesmosomes which connect with the extracellular organic film (Figure 5E). Macroscopically, these cells appear to be connected with the extrinsic muscle fibers (Figure 4).

The interstitial tissue of the projection surrounded by the outer epithelium is filled with connective tissue and extrinsic muscle fibers (Figure 4). Several amoebocytes, $10\text{--}20\text{ }\mu\text{m}$ in diameter, occur in these connective tissues. Crystal spherules, which attain $100\text{ }\mu\text{m}$ in diameter, occasionally occur in this connective tissue. No characteristic cells surrounding such spherules are found.

Organic materials of various sizes and shapes (fibrous, granular, membrane) are observed within the tubule (Figure 6). The fibrous material is common and abuts the prismatic wall of the tubule. Many organic granules ($0.2\text{--}6.0\text{ }\mu\text{m}$ in diameter) occasionally occur in the tubule (Figure 6A). These granules appear to change gradually from membranelike sheets to fibrous materials at the boundary of the prismatic wall of the tubule (Figure 6B). The structure of these organic materials at the boundary of the shell wall exhibits a characteristic dendritic appearance (Figure 6B). Although these organic materials exist in the tubules of all examined specimens regardless of the presence or absence of shell dissolution, they are more abundant in large tubules in the specimens with extensive shell dissolution than in small tubules in the specimens without shell dissolution.

DISCUSSION

Formation and Functions of Organic Sheets

Judging from the histological and histochemical staining tests for the comparison between organic sheets and periostracum of *Geloina*, organic sheets appear to be similar in composition to the outer layer of periostracum, although

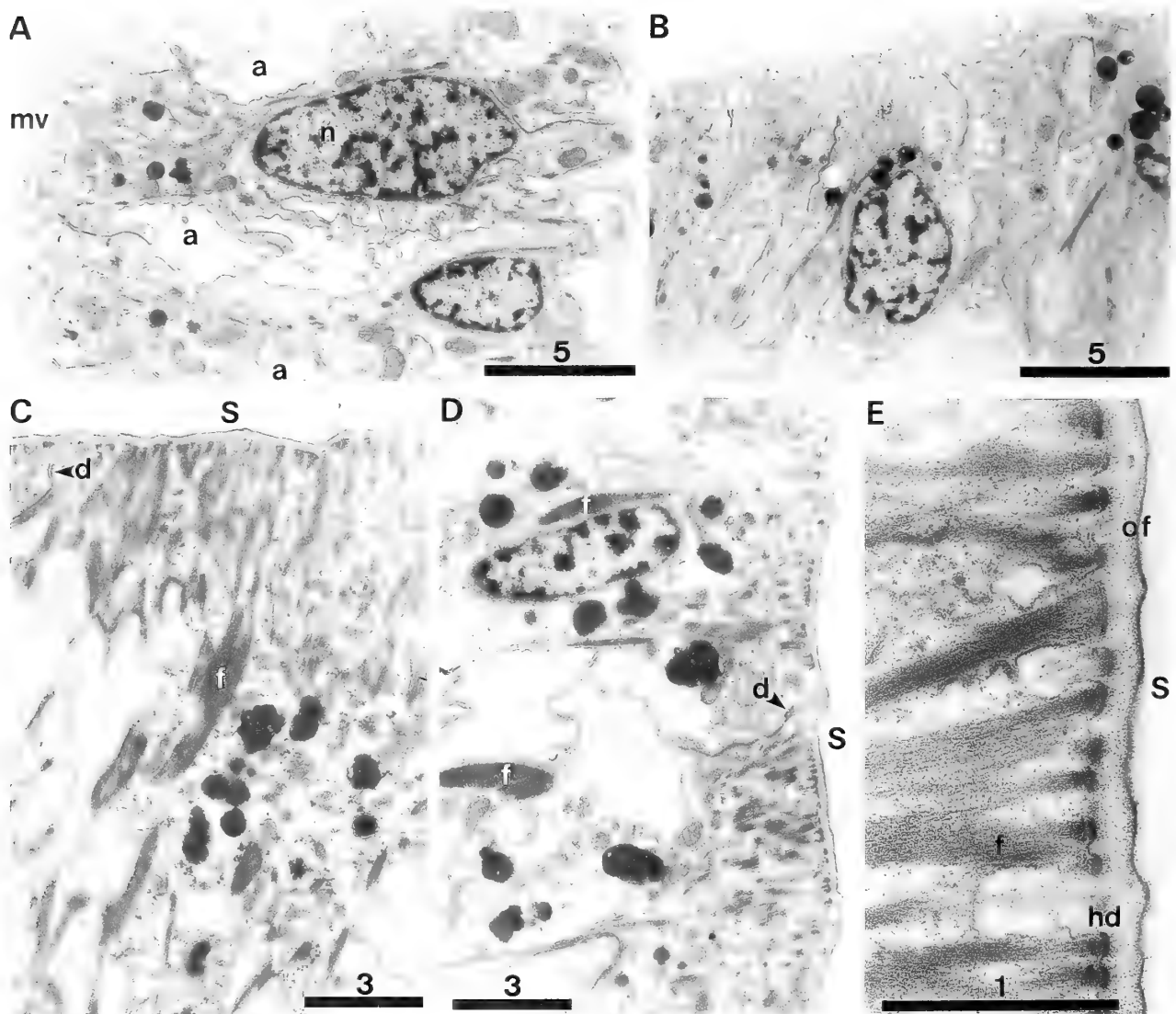


Figure 5

Transmission electron micrographs showing epithelial cells situated at the umbonal region of the outer mantle epithelium. (A) Epithelial cells at the tip of projection. (B) Epithelial cells at the general mantle surface. (C, D) Adhesive epithelial cells at the lateral surface of projection. (E) Enlarged view of the apical end of an adhesive epithelial cell. a: artifact; d: desmosome; f: fibrils; hd: hemidesmosome; mv: microvilli; n: nucleus; of: organic film; S: the area where the shell was. Scale in microns.

precise amino acid composition was not examined. In addition, organic sheets retard shell dissolution when they are exposed on eroded surfaces. This role is analogous to the periostracum, indicating that internal organic sheets may have high hydrophobicity.

Most shell repair experiments show that periostracumlike organic sheets are secreted primarily from the general outer mantle epithelium in the injury area of shell. These reactions of the exposed mantle are a direct result of contact with a changed environment (Tsuji, 1960, 1976; Kawaguchi & Ikemoto, 1962; Beedham, 1965; Meenakshi

et al., 1973; Uozumi & Suzuki, 1979). These experiments have also demonstrated that accompanying morphological changes of the mantle epithelium are drastic in the mid-shell regions inside the pallial line. In *Anodonta* and *Musculus*, the epithelium, which is normally composed of simple cuboidal cells and secretes the nacreous layer, is transformed into simple columnar cells as in those of the outer fold of the mantle edge (Tsuji, 1960, 1976; Kawaguchi & Ikemoto, 1962; Beedham, 1965). In addition, during shell repair, the general outer mantle epithelium can secrete in succession non-calcareous as well as calcified com-

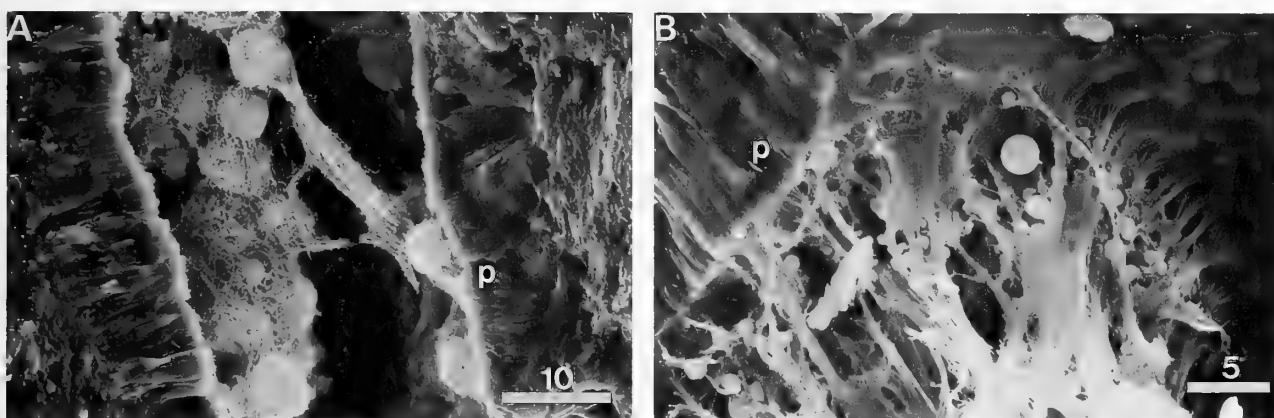


Figure 6

Scanning electron micrographs showing organic materials in the tubules. (A) Organic granules in the specimen without shell dissolution. (B) Organic materials in the specimen with extensive shell dissolution. p: prismatic wall of a tubule. Scale in microns.

ponents of some layers of the valves. Shell repair experiments therefore indicate that there is no absolute difference in secretory properties among the various epithelial zones of the mantle, and that the function of the mantle epithelium is not permanently fixed, but can be altered by a stimulus such as shell damage (Beedham, 1965; Watabe, 1983). As reported by Wada (1976), however, who investigated the amino acid composition of anomalous organic materials secreted on the inner shell surface of *Pinctada fucata* by the infection of Polychaeta, organic materials secreted from the general outer mantle surface inside the pallial line are different from periostracum in structural, compositional, and formational aspects. Therefore, outer mantle epithelium inside the pallial line appears to have no ability to secrete true periostracum.

In the case of *Geloina*, it is clear that organic sheets within the shell are secreted from the stimulated underlying epithelial cells, which are concerned solely with the formation of complex crossed lamellar structure unless they are stimulated by shell dissolution. At present, it is unclear whether organic sheets of *Geloina* are abnormally secreted under anomalous conditions or are alternately secreted as one of variable secretory conditions by stimulated epithelial cells. Prismlike and/or granular structures underlying the organic sheets appear to be formed during the transitional stage from organic to calcified materials.

When shell dissolution occurs in acidic environments, boring by endolithic microorganisms can occur into the shell from the eroded surface (up to 3 mm in depth) (Figure 7). It seems likely that organic sheets are secreted from underlying epithelial cells as a response to stimuli which are transmitted through the boring formed by endolithic microorganisms when it reaches the inner shell surface. However, the response of organisms to rapid shell removal in shell repair experiments may be somewhat different from the case of *Geloina*, because the natural shell dissolution must be slow.

The primary role of organic sheets in shells undergoing extensive shell dissolution is interpreted to be coating the openings of boring of microorganisms (Figure 7A). Taking the results of shell repair experiments into consideration, the important role of organic sheets in retarding the rate of shell dissolution may have been achieved secondarily when the organic sheet was exposed on the eroded surface (Figure 7B). As a result of formation of organic sheets by *Geloina*, the secondary role of organic sheets in preventing shell dissolution was favored for survival in acidic mangrove swamps in which shell dissolution occurs frequently.

It is unknown whether the ability of the general mantle epithelium to secrete organic sheets during shell repair exists in all bivalves. Our knowledge of shell repair processes comes mainly from a few limited taxa with a thick periostracum, such as *Anodonta* (Tsujii, 1960; Beedham, 1965) and *Mytilus* (Meenakshi et al., 1973; Uozumi & Suzuki, 1979).

Judging from the similarities between organic sheets and periostracum, there is a possibility that bivalves with a thick periostracum have an ability to secrete organic sheets from the general mantle epithelium in response to shell dissolution. However, no internal organic sheets have been observed in large specimens of brackish to freshwater corbiculids such as *Corbicula leana*, *C. sandai*, and *C. japonica*, all of which have a thick periostracum and extensive dissolution in their umbonal region. These facts indicate that secretion of organic sheets may not be a universal response in bivalves to shell dissolution. Therefore, the ability to secrete organic sheets in *Geloina* probably arose from the process of adaptation to acidic mangrove environments.

Formation and Functions of Tubules

In all *Geloina* specimens with extensive shell dissolution in their umbonal region, tubules occur locally within the

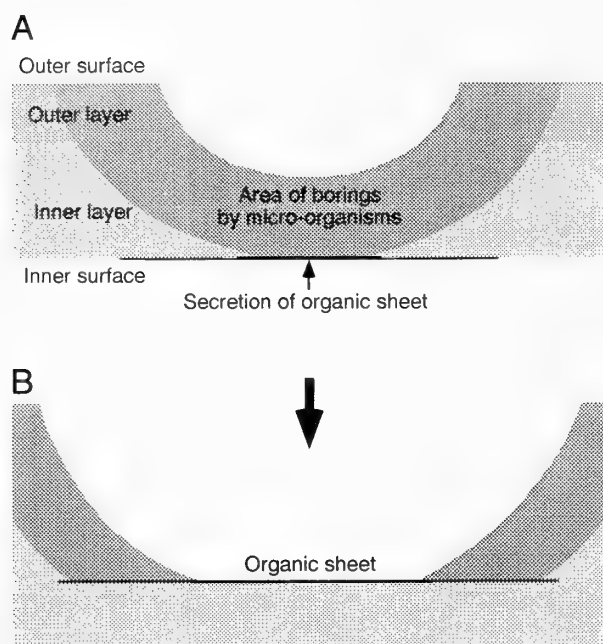


Figure 7

Schematic diagram showing the process of shell dissolution and secretion of organic sheet in the ventral region without tubules. (A) Boring of endolithic microorganisms occurs from the eroded surface (up to 3 mm in depth). (B) An organic sheet is exposed on the eroded surface. An organic sheet is secreted from the general mantle epithelium when they are stimulated by borings of microorganisms. Depositional surface is toward the bottom.

inner shell layer in association with many internal organic sheets. This correlation suggests that the tubules are somehow related to the formation of internal organic sheets. It is predictable that secretion of organic sheets in the umbonal region may be different from that in the other shell area without tubules.

When the boring by microorganisms reaches the top of tubules in the umbonal region, the stimulus may be transmitted from the external environment to the extrapallial space through the tubules (Figure 8). For this reason, when shallow dissolution occurs in the umbonal region of the shell, the animals appear to secrete the organic sheets before shell dissolution reaches the inner side. Therefore, it may safely be assumed that tubules of *Geloina* are involved in effecting the secretion of organic sheets in response to shell dissolution. Similar secretion of organic layers prior to complete penetration of dissolution was reported by Tevesz and Carter (1980) and called "prophylaxis layers."

Tubules are formed toward the inner side of the shell, contemporaneously with shell deposition (Figure 8). Epithelial cells on the umbonal region have resulted in the formation of tubules. However, no reliable morphological criterion even at the ultrastructural level has yet been found to determine their function. Therefore, it is necessary to

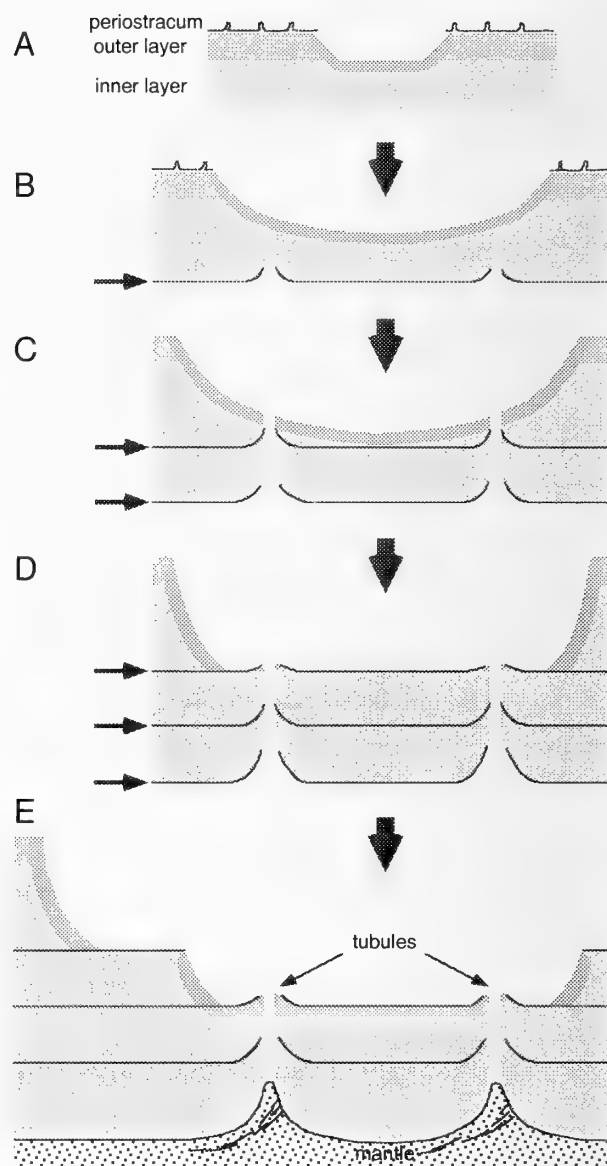


Figure 8

Schematic diagram showing the process of secretion of organic sheets in the umbonal region. (A) Shell dissolution occurs on the outer shell surface in the umbonal region. (B) Microboring reaches the top of tubules. An organic sheet is secreted (horizontal arrow) from the outer epithelium when the stimulus of shell dissolution reaches the mantle projection. (C, D) The epithelium secretes an organic sheet temporarily during the course of secretion of the inner complex crossed lamellar shell layer. From A to E, tubules are formed toward the inner side of the shell, contemporaneous with shell deposition. Prismlike or granular shell structures just beneath the organic sheet are not figured. Depositional surface is toward the bottom.

determine the function by both the morphology and secretion of the cell.

Secretory functions of epithelial cells situated on the tip of the projection are closely related to the formation of

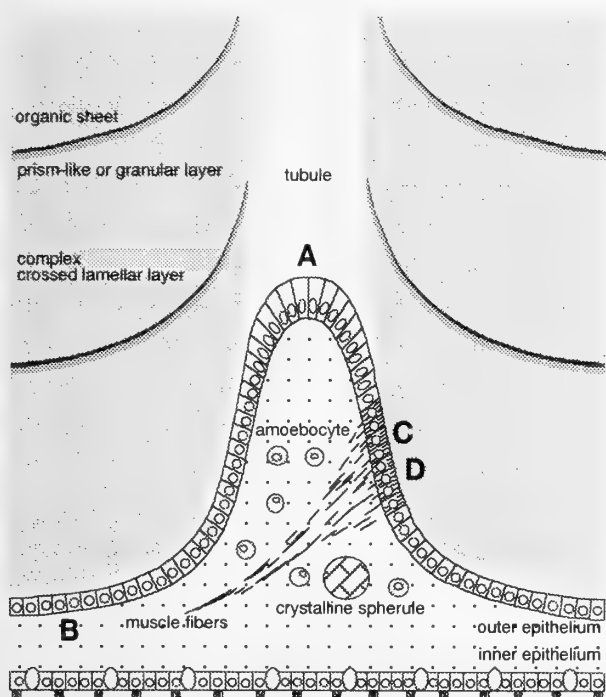


Figure 9

Schematic figure of a mantle projection. Epithelial cells (A, B, C, D) are figured in Figure 5 (A, B, C, D). Organic sheet is formed by the secretory activity of the general epithelial cell (B). Prismatic wall of a tubule is not figured. Depositional surface is toward the bottom.

tubules (Figure 9). This portion consists of simple columnar cells which resemble epithelial cells secreting organic sheets in shell repair experiments (Tsuji, 1960, 1976; Kawaguchi & Ikemoto, 1962; Beedham, 1965). These epithelial cells secrete organic materials in a tubule with or without shell dissolution. Judging from the existence of a tubule over the tip of the projection, these epithelial cells may not secrete calcified shell material. Based on these assumptions, it seems reasonable to suppose that the epithelial cells situated on the tip of the projections are differentiated in function.

Epithelial cells on the lateral side of projections have characteristic bundles of fibrils. These cells are closely similar to the muscle attachments described for gastropods by Tompa & Watabe (1976). The fibrils within the epithelial cells appear to be tegumental fibers. Waller (1980) reported similar structures in the pallial adhesive epithelium of *Glycymeris glycymeris* by SEM. Therefore, this portion of the outer epithelium may provide a mechanical anchor for the extrinsic muscle fibers in the connective tissue to the inner shell surface, suggesting that these cells represent adhesive epithelium. Indeed, these cells are damaged when the mantle is stripped from the shell. These bundles of fibrils within the cell are similar to those in the epithelium observed in *Mytilus* (Bubel, 1973) and of bec-

cublast cells within the buccal masses of some cephalopods (Dilly & Nixon, 1976).

In addition to histological features mentioned above, some amoebocytes and crystalline spherules exist in the connective tissue in the mantle of the umbonal region (Figure 9). Several authors assumed that these amoebocytes in the stimulated area of the mantle in bivalves and gastropods serve for protection, ingestion, transportation of material, and secretion of a periostracumlike membrane (Wagge, 1951; Beedham, 1965; Nakahara & Bevelander, 1967; Tsujii, 1976). In *Geloina*, amoebocytes may play the same roles mentioned above in wound healing at the mantle projection, which appear to be stimulated by shell dissolution. Several authors also reported extracellular crystalline spherules in the mantle of bivalves. Calcium carbonate spherules are well known to occur in the interstitial tissue of the mantle of freshwater bivalves (Istin & Girard, 1970; Simkiss, 1976). According to Wada (1980, 1988), the activity product $a\text{Ca}^{2+} \cdot a\text{CO}_3^{2-}$ in the interstitial tissue of marine species is much smaller than in freshwater species. For this reason, calcium carbonate precipitation may take place more readily in the tissue and extrapallial fluid of freshwater species. If Ca^{2+} concentration is closely connected to the formation of crystalline spherules in the connective tissue, crystalline spherules of *Geloina* may be formed at the onset of shell repair. Enlargement of the mantle projection in the specimens with extensive shell dissolution may be connected to the Ca^{2+} concentration in the connective tissue. At present, little is known about the mineralogy and structure of crystalline spherules in the connective tissue of *Geloina*.

Available data from histological and ultrastructural studies indicate that epithelial cells situated on the tip of a projection may be uniquely differentiated to form tubules, and that mantle projection appears to be involved in the adhesion of tissue to the inner shell surface (Figure 9). Therefore, the mantle projection in the umbonal region of *Geloina*, which is initially a shell adhesive tissue, may be regarded as an exaptation (Gould & Vrba, 1982).

Molluscan epithelium contains numerous sensory receptor cells. A large number of studies conducted on the epithelial sensory receptor cells of mantle edge in gastropods, especially in the Pulmonata (Crisp, 1971; Zylstra, 1972; Zylstra et al., 1978; Wondrak, 1975; Jones & Saleuddin, 1978). Jones & Saleuddin (1978) and Zylstra et al. (1978) identified several types of receptor cells involved in controlling repair at the shell edge in *Helisoma duryi*, *Lymnaea stagnalis*, and *Biomphalaria pfeifferi*. No studies exist concerning the control mechanisms relative to repair in the mid-shell regions or in any region of bivalves (Watabe, 1983, personal communication). In this study, no epithelial sensory cells have been observed in the outer mantle epithelium inside the pallial line. This result is consistent with previous observations that receptor cells occur in a certain sensitive area, which is usually exposed (Bullock & Horridge, 1965; Crisp, 1971; Zylstra, 1972). This fact indicates that the stimulus of shell dissolution,

either mechanical or chemical and/or by microorganisms, is received by the general epithelial cells having no specific morphological criteria (e.g., cilia, numerous number of elongate microvilli).

Tubules in Other Bivalves

Although the mode of distribution of tubules has been investigated by previous workers, little is known about the ultrastructural features of soft tissue and its function. Most tubules in various taxa penetrate both the inner and outer shell layers (Arcoida: Oberling, 1955, 1964; Omori et al., 1962; Wise, 1971; Waller, 1980; Shibata, 1980; Spondyliidae: Oberling, 1964; Omori & Kobayashi, 1963; Carditidae: Oberling, 1964; Dreissenidae: Pathy & Mackie, 1993; Pisidiidae: Rosso, 1954; Robertson & Coney, 1979; Lyonsidae: Oberling, 1964). Especially in the case of Arcoida, tubules are formed by a projection of a single cell after calcified material was deposited. In this respect, they are quite different from the tubules in *Geloina*, which are formed contemporaneous with shell deposition. Tan Tiu & Prezant (1989) reported shell tubules in *Corbicula fluminea*. The distribution of shell tubules in this species is restricted to the early dissoconch as in *Geloina*; however, the diameter and morphology of shell tubules are different from *Geloina*. They proposed that supplementary anchorage of mantle to shell is the primary function of the tubule tissues in *C. fluminea*. No observations have been made for these other species by TEM.

The taxonomic distribution of tubules in bivalves is very interesting. According to Oberling (1964) and Waller (1980), the tubules are common in many distantly related epifaunal bivalves but are rare in infaunal taxa. Pathy & Mackie (1993) reported that the mode of distribution of canal structure is quite different among the three dreissenids, *Dreissena polymorpha*, *Mytilopsis leucophaeata*, and the "quagga" mussel. These facts suggest that tubules are an unstable feature within a monophyletic group and may be polyphyletic in origin. Ultrastructural examination of the contained soft tissues is needed to determine the origin and function of the tubules.

Other Bivalves Inhabiting Acidic Environments

As stated above, the secretion of organic sheets in *Geloina* is interpreted to be an ecophenotypic response to shell dissolution. As already stated by previous workers, organic sheets within the shell are ubiquitous among freshwater species of the Unionoidea. Extensively eroded shells have more numerous organic sheets than the shells without appreciable umbonal dissolution (Tevesz & Carter, 1980; Kat, 1983). However, organic sheets in the inner nacreous layer of some Unionoidea (e.g., *Anodonta*, *Elliptio*, *Lampsilis*) appear to show cyclic distribution and to be consistent in number with external thick growth bands (Nelson, 1964). Based on the assumption that thick growth bands in some Unionoidea are formed annually, some authors have regarded organic sheets within the inner nacreous layer as

also annual (Nelson, 1964). There is a possibility that organic sheets within the inner nacreous layer of some species of the Unionoidea are secreted annually by the outer mantle epithelium regardless of shell dissolution. Annual fluctuations of the chemical setting in habitat may be closely related to the formation of internal organic sheets in some Unionoidea. In addition, they have no associated tubules. The formation of organic sheets within unionids' shell should be studied further in detail. If the above assumption is confirmed, the different mechanisms between *Geloina* and some unionids may be attributed to their phylogenetic distance and different adaptive evolutionary history.

Internal organic sheets do not necessarily occur in all the bivalves inhabiting acidic environments. Indeed, the Dreissenidae, Corbiculidae (except for *Geloina*) and Pisidiidae have no internal organic sheets within their shells in spite of their obvious success in freshwater environments (McMahon, 1983; Mackie, 1984; Kat, 1985). These bivalves may adopt different strategies for life in acidic environments. For instance, reproductive strategies seem to be more important in the family Pisidiidae. The majority of the species belonging to Pisidiidae are semelparous having a 1-year life span, and the parents die after the first spatfall. Therefore, these bivalves may have not undergone extensive shell dissolution during their short life span. It is unlikely that shell dissolution functions as a selective agent among bivalves having a short life span and rapid replacement of one generation by another.

Concluding Remarks

Organic sheets within bivalve shells prevent lethal shell dissolution. This feature exists in several distantly related bivalves inhabiting acidic environments (Kat, 1985), and also in the neritid gastropod *Clithon retropictus*, which undergoes extensive dissolution in the apical portion (S. Isaji, unpublished data). Therefore, organic sheets can be interpreted as an adaptive feature for acidic environments, in which shell dissolution may be an agent of selection.

The secretion of organic sheets in *Geloina* is an adaptive response to shell dissolution, though *Geloina* appears to have no specific receptor cells concerned with the detection of shell dissolution. However, many pulmonate gastropods have epithelial receptor cells in the mantle which could be concerned with the control mechanisms of shell repair. It is inferred that the differences between the peripheral nervous systems of bivalves and gastropods may have arisen in relation to their different mode of feeding and locomotion.

Analysis of the adaptation of bivalves to acidic environments is important for understanding the invasion of marine mollusks into freshwater settings. According to Hutchinson (1967) and Gray (1988), in some tropical regions such as Indo-Malaysia, West Africa, and tropical America, several predominantly marine stocks have one or a few freshwater representatives. In those tropical regions, stable

temperature, abundant rainfall, and low salinity gradients seem to have been important for bivalves adapting to freshwater (Gray, 1988). In the case of mangrove swamps, physico-chemical conditions are more severe than shallow marine environments, and molluscan diversity is much decreased. In these respects, mangrove swamps may be comparable with freshwater environments, although water conditions are different between them. If physico-chemical barriers are critical for the invasion of marine bivalves into acidic and freshwater environments, it is likely that the problem of invasion has been solved separately in different groups of bivalves by means of adaptive changes against non-biological agents of selection.

ACKNOWLEDGMENTS

I wish to thank Professor Itaru Hayami (Kanagawa University), Professor Kazushige Tanabe (University of Tokyo), and Professor Koji Wada (Mie University) for critical review of the manuscript and for valuable comments. I am also grateful to Drs. Katsumi Abe (Shizuoka University) and Tatsuo Oji (University of Tokyo) for many helpful suggestions during the course of this work. My special thanks are due to Dr. Tsuguo Otake (Ocean Research Institute, University of Tokyo) for his assistance in preparing the material for TEM observation. Thanks are also due to the Research Institute of Tropical Agriculture, University of the Ryukyus for providing support during fieldwork in Iriomote Island.

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Self-Fertilization versus Cross-Fertilization in Two Planorbid Species, *Planorbarius corneus* (Linnaeus) and *Planorbis planorbis* (Linnaeus)

by

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Abstract. Individuals of two planorbid species, *Planorbarius corneus* (Linnaeus) and *Planorbis planorbis* (Linnaeus), were isolated from hatching at various constant temperatures (10, 15, 20, and 25°C) to test their selfing ability. At 15°C and above, both species produced egg capsules, but many of them contained few or no eggs.

In *P. planorbis*, the mean number of eggs per capsule was maximal (2.1) at 20°C, but only two embryos were produced and these did not develop. Thus, *P. planorbis* cannot be considered as a self-fertile species in the rearing conditions of the present experiments.

By contrast, *P. corneus* can reproduce by self-fertilization. Nevertheless, the snails laid few egg capsules (on average, 20.1 ± 15.1 capsules throughout the reproductive period at 20°C) which contained very few eggs (1.3 ± 2.3) including very few embryos (1.1 ± 2.1). Moreover, the hatching rates were low (5 to 6%).

Compared with grouped individuals, the isolated snails of both species showed a great reduction in fecundity (95% and 98.5% in *P. corneus*; 99.9 and 100% in *P. planorbis*).

INTRODUCTION

Planorbarius corneus (Linnaeus, 1758) and *Planorbis planorbis* (Linnaeus, 1758) are simultaneous hermaphrodites, like all basommatophorans. Although outcrossing is the usual mode of reproduction, the occurrence of both selfing and outcrossing has been reported in about 50 basommatophoran species (Vianey-Liaud, 1990), including the planorbid species: *Armiger crista* (Linnaeus) (Alfaro-Tejera, 1982), *Helisoma duryi* (Weatherby) and *Helisoma trivolvis* (Say) (Paraense & Correa, 1988), *Biomphalaria glabrata* (Say) (Brumpt, 1941), *Biomphalaria pfeifferi* (Krauss) (Vianey-Liaud, 1984), and *Bulinus cernicus* (Morelet) (Rollinson et al., 1989). Laremborgue (1939) and Brumpt (1941) also gave lists of self-fertile basommatophoran species. In *B. glabrata*, Paraense (1976) has demonstrated that outcrossing occurs in the ovotestis, whereas selfing takes place in the seminal vesicles. As a general rule, snails switch rapidly to cross-fertilization after pairing. The prevalence of cross-fertilization over self-fertilization is suggested by the genotypic frequencies at polymorphic loci,

which show a close fit to Hardy-Weinberg expectations (for review, see Jarne et al., 1993). However, research has shown that individuals in some land pulmonate species self-fertilize frequently and have little or no detectable heterozygosity, and this mode might be a strategy for assembling and conserving adaptive genomes (see McCracken & Brussard, 1980).

Self-fertilization has been reported by Holzfuss (1914) and Allen (1935) in *P. corneus* and by Holzfuss (1914) in *P. planorbis*. The aim of this study was to verify the ability of self-fertilization in these two species and to examine the influence of the temperatures recorded in our area during the snail reproductive period on this mode of reproduction. The fecundities of isolated and grouped snails were compared for different rearing temperatures.

MATERIALS AND METHODS

The snails used in our experiments were born in the laboratory from parents collected in two ponds located near Rennes (Brittany, France). They were isolated 2 weeks

after hatching, and each individual was kept in an aquarium filled with 950 mL of pond water. Four temperature treatments (10, 15, 20, and 25°C) were tested for both species. Unfortunately, accidental meetings between individuals of *P. corneus* reared at 15°C forced us to eliminate the results at this temperature. At each temperature and for both species, 10 individuals were chosen at random for experiment. The snails were fed with fresh lettuce *ad libitum*. The photoperiod was 12 hrs light/12 hrs dark.

Every other day, the egg capsules were collected; every week the eggs were counted under a stereo microscope, and the survivors counted. Moreover, the eggs were examined in order to determine if they contained embryos (egg cells) or not (Figure 1). The egg capsules which contained embryos were incubated at the temperature at which they had been produced. Each experiment continued until the death of the last snail.

For each temperature and species, the following parameters were determined: the number of isolated individuals laying egg capsules out of 10 experimental snails; the mean, shortest, and longest snail longevities; the mean and earliest ages at the onset of egg laying; the mean numbers of egg capsules (including eggs and lacking eggs) per snail throughout life span and per reproductive week; the mean numbers of eggs and embryos per egg capsule; the percentage of egg hatching; the mean fecundity of snails: mean number of embryos laid per snail throughout its life span.

The results for isolated snails were compared with those obtained in grouped snails (Costil & Daguzan, 1994). These comparisons have to be done with caution for three main reasons: (1) the effect of density cannot be dissociated from results produced by different modes of fertilization; (2) for each temperature, the observations were made on 68 (*P. corneus*) or 80 (*P. planorbis*) grouped snails (divided

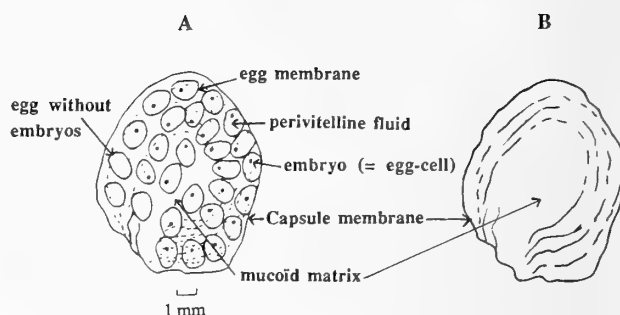


Figure 1

Egg capsules (A) containing some eggs which are without embryos or (B) containing no eggs in *Planorbarius corneus*.

into four sets for each species) and only on 10 isolated snails; (3) results with the isolated snails were individual, whereas they were expressed as means \pm standard deviation (SD) in the case of grouped snails.

RESULTS

At 10°C, no egg capsules were laid by the isolated individuals of either species, but capsules were obtained at higher temperatures. Out of 10 experimental snails, more reproducing snails were observed for *Planorbarius corneus* (nine and 10 snails) than for *Planorbis planorbis* (seven at the most) (Table 1). Nevertheless, the rates of fertile snails did not differ significantly between the two species ($\chi^2 = 1.25$ and $\chi^2 = 3.53$, respectively, for 20°C and 25°C). The first species lived longer than the latter. The mean longevities of isolated and grouped snails differed significantly (see results of Mann & Whitney tests): the isolated snails

Table 1

Longevity of isolated and grouped individuals of *Planorbarius corneus* and *Planorbis planorbis* according to temperature. Differences between the longevities of the 10 isolated and the grouped snails are expressed by the values of Z (which indicate the significance level of differences, according to the Mann-Whitney test). Mean (m) \pm standard deviation (SD).

*: $P < 0.001$; NS: non-significant.

	<i>Planorbarius corneus</i>		<i>Planorbis planorbis</i>		
	20°C	25°C	15°C	20°C	25°C
Number of isolated individuals laying egg capsules out of 10 experimental snails	9	10	3	7	7
Age when the first and the last isolated snail died (weeks)	51–162	39–115	18–101	11–56	15–32
Mean longevity of the isolated individuals which reproduced (\pm SD) (weeks)	128 \pm 36	100 \pm 22	94 \pm 7	23 \pm 8	25 \pm 5
Mean longevity of the 10 isolated snails (\pm SD) (weeks)	120 \pm 42	100 \pm 22	46 \pm 34	28 \pm 13	19 \pm 9
Mean longevity of the grouped snails (\pm SD) (weeks)	96 \pm 54	58 \pm 33	101 \pm 43	49 \pm 18	19 \pm 9
Z	–1.6 ^{NS}	–4*	–3.3*	–3.4*	–1.3 ^{NS}

Table 2

Mean age at the onset of sexual maturity of isolated and grouped individuals of *Planorbarius corneus* and *Planorbis planorbis* according to temperature. Mean (m) \pm standard deviation (SD); n = number of snails reaching sexual maturity.

	<i>Planorbarius corneus</i>		<i>Planorbis planorbis</i>		
	20°C	25°C	15°C	20°C	25°C
Mean age of the isolated individuals at the onset of sexual maturity (\pm SD) (weeks)	19 \pm 3 (n = 9)	25 \pm 5 (n = 10)	45 \pm 9 (n = 3)	14 \pm 6 (n = 7)	18 \pm 4 (n = 7)
Age of the earliest isolated snail (weeks)	16	19	32	9	14
Age of the earliest grouped snail (weeks)	17	15	15	11	9

of *P. corneus* lived longer than the grouped individuals, whereas the reverse result was found for *P. planorbis* at 15 and 20°C but not at 25°C.

The higher the temperature, the earlier the egg capsules were laid by the grouped snails. The more precocious isolated individuals were those kept at 20°C (mean ages of 19 and 14 weeks for *P. corneus* and *P. planorbis*, respectively) (Table 2). At a given temperature, great variation in the number of egg capsules occurred among isolated individuals. For example, the total number of capsules laid by the individuals of *P. corneus* reared at 20°C ranged from three to 49 capsules (Table 3). The highest mean numbers of egg capsules produced throughout the life span were observed at 20°C in *P. corneus* and at 15°C in *P. planorbis* (20.1 \pm 15.1 and 13.3 \pm 19.6, respectively) (Table 4). However, if the capsule production is considered per reproductive week, *P. planorbis* snails were the most productive at 20°C (1.0 capsule per snail and per reproductive week).

The maximum numbers of eggs per capsule reached 15 eggs for *P. corneus* and 12 eggs for *P. planorbis*, but a large proportion of capsules were without eggs, especially in *P. planorbis* (from 52.6% to 95%) (Table 4). The capsules laid by the isolated snails contained far fewer eggs than those produced by grouped snails. Actually, the reduction

in number of eggs per capsule reached 91% in *P. corneus* (at 20°C) and 99% in *P. planorbis* (at 15°C). Moreover, none of the eggs in the capsules laid by *P. planorbis* reared at 20 and 25°C contained egg cells, i.e., were without embryos. At 15°C, a single embryo was observed in only two different capsules. In *P. corneus*, the capsules rarely held more than two eggs, and 26% of the masses laid at 20 and 25°C contained non-embryonated eggs. The mean number of embryos per capsule was close to one at both temperatures.

The maximum mean fecundities of isolated individuals of *P. corneus* and *P. planorbis* were 21.8 and 0.7 embryos, respectively (Table 5). If we compare the fecundities of isolated snails with those of grouped snails, this is a reduction of between 95% and 100%. The two embryos of *P. planorbis* put to incubate did not develop, while the hatching rates for *P. corneus* were low: 5.2% (25°C) and 6.1% (20°C) (Table 4). During the experiment, only four newly hatched snails (each from a different capsule) and 12 young snails (five of which came from the same capsule) were achieved at 25 and 20°C, respectively.

DISCUSSION

To be relevant, the isolation experiments have to be started out using very young immature snails because of allosperm storing, sometimes for up to several months (Rudolph & Bailey, 1985; Vianey-Liaud, 1990; Wethington & Dillon, 1991). For example, *Anisus vortex* (Linnaeus) was considered to be a self-fertile species by Chadwick (1903), but the isolation of experimental snails was not carried out early enough to be certain about this conclusion. Freshwater snail biology can be influenced by many factors such as food availability and temperature, and a complicating factor is the advantage of varying temperatures in comparison with constant temperatures (Hodasi, 1976; Aboul Ela & Beddiny, 1980). In the present study, the individuals were kept under good feeding conditions allowing them to grow normally. Nevertheless, the results have to be considered in relation to the rearing conditions.

In the present experiments, the isolated snails of both species reared at 10°C did not reproduce in spite of a good survivorship. This was also the case for grouped *Planorbarius corneus* kept at this temperature, which seems to

Table 3

Egg capsule production in 10 individuals of *Planorbarius corneus* and *Planorbis planorbis* reared at different temperatures throughout life span. The snails in each group are arranged according to increasing egg-capsule production.

	Temperature	Number of the various individuals (10 per temperature)									
		1	2	3	4	5	6	7	8	9	10
<i>P. corneus</i>	20°C	0	3	9	10	11	17	21	24	39	49
	25°C	1	2	2	6	6	8	14	14	16	16
<i>P. planorbis</i>	15°C	0	0	0	0	0	0	0	2	2	36
	20°C	0	0	0	1	1	2	2	9	10	13
	25°C	0	0	0	1	1	2	4	4	16	24

Table 4

Production of egg capsules, eggs and embryos by the isolated individuals of *Planorbarius corneus* and *Planorbis planorbis* reared at different temperatures. Mean (m) \pm standard deviation (SD). *: all egg capsules (including eggs or lacking eggs) are considered; **: eggs lacking embryos are excluded from the tallies.

	<i>Planorbarius corneus</i>		<i>Planorbis planorbis</i>		
	20°C	25°C	15°C	20°C	25°C
Mean number of egg capsules produced per isolated individual throughout life span (\pm SD)*	20.1 \pm 15.1	8.5 \pm 6.0	13.3 \pm 19.6	5.4 \pm 5.1	7.4 \pm 8.9
Mean number of egg capsules produced per isolated individual per reproductive week (\pm SD)*	0.20 \pm 0.13	0.11 \pm 0.07	0.35 \pm 0.49	1.00 \pm 0.93	0.83 \pm 0.79
Percentage of capsules without eggs laid by the isolated snails	40.4%	18.8%	95%	52.6%	90.4%
Mean number of eggs per egg capsule in the isolated snails (\pm SD)	1.31 \pm 2.27	1.23 \pm 0.96	0.15 \pm 0.53	2.10 \pm 3.16	0.21 \pm 0.99
Mean number of eggs per egg capsule in the grouped snails (\pm SD)	14.8 \pm 4.8	10.1 \pm 7.1	14.9 \pm 3.8	18.4 \pm 6.1	8.6 \pm 5.0
Mean number of embryos per egg capsule in the isolated snail (\pm SD)	1.07 \pm 2.07	0.90 \pm 0.98	0.05 \pm 0.22	0	0
Hatching percentage of eggs produced by the isolated snail**	6.1%	5.2%	0%	—	—

prevent sexual maturity in this species (Costil & Daguzan, 1994). On the other hand, the grouped *Planorbis planorbis* laid egg capsules at 10°C. Such a difference between grouped and isolated snails could be due to a crowding effect if snail grouping favors reproduction. At 15°C, only three isolated individuals of *P. planorbis* laid eggs, and this low number can be related to the short life span at this temperature. In contrast, snails which laid eggs lived on for 94.0 weeks (SD = 7.0) and became mature at the mean age of 56.0 weeks (SD = 21.6); those which did not reproduce had a shorter mean life span of 25.7 weeks (SD = 8.8). The large mortality of the isolated snails at 15°C is quite surprising in view of the long life span of grouped snails at the same temperature (Costil, 1994). Except for *P. planorbis* reared at 15°C, the onset of sexual maturity was similar in both isolated snails and grouped snails, the differences never going beyond 5 weeks. By contrast, Van Duivenboden (1983) in *Lymnaea stagnalis* (Linnaeus) and

Jarne et al. (1991) in *Bulinus globosus* (Morelet) observed that isolation delayed the onset of egg laying.

In the present study, *P. planorbis* kept in isolation produced few egg capsules which contained very few eggs and no embryos (with the exception of two eggs each showing one embryo). Therefore, we can conclude that *P. planorbis* cannot be considered as a self-fertile species. Larambergue (1939) found a similar result for the closely related species, *Planorbis carinatus* (Müller).

In *P. corneus*, only a few capsules poor in eggs and in embryos, and only 16 newly hatched snails were attained in total; great reduction in fecundity (at least 95%) was then observed in isolated snails when compared to grouped snails. Allen (1935) has recorded a similar result for one individual of this species: seven capsules, some of which were sterile and which gave birth to only five young snails during a period of 3 years. Although greater fecundities have been reported in isolated snails than in grouped snails,

Table 5

Comparison of the mean fecundities (\pm standard deviation) in isolated and grouped individuals of *Planorbarius corneus* and *Planorbis planorbis* reaching sexual maturity and reared at different temperatures. (n) = number of snails reaching sexual maturity.

	<i>Planorbarius corneus</i>		<i>Planorbis planorbis</i>		
	20°C	25°C	15°C	20°C	25°C
Mean number of embryos produced per isolated snail throughout the life span	21.8 \pm 18.4 (9)	7.7 \pm 8.2 (10)	0.7 \pm 1.2 (3)	0 (7)	0 (7)
Mean number of embryos produced per grouped snail throughout the life span	1453 (57)	148 (54)	2951 (73)	1943 (74)	81 (71)
Fecundity reduction (in %)	98.5%	95%	99.9%	100%	100%

for example, in *Lymnaea stagnalis* (Van Duivenboden et al., 1985) and in *Bulinus truncatus* (Audouin) (Bayomy & Joosse, 1987), the reverse appears to be more common. In *Lymnaea peregra* (Müller), an inbreeding depression of 90% (including both fertility and viability) was emphasized by Jarne & Delay (1990). In *Bulinus cernicus*, 10.8% of the isolated snails did not lay eggs, and the egg masses from snails which had self-fertilized tended to be smaller than those laid by cross-fertilizing snails (3.67 eggs per egg capsule as opposed to 5.34) (Rollinson et al., 1989). In the land snail, *Triodopsis albolabris* (Say), the reproductive success of paired individuals was about 86 times greater than that of isolates (McCracken & Brussard, 1980). Moreover in the present study, hatching rates were very low for *P. corneus* (5 and 6%), whereas they ranged from 37.3% (at 10°C) to 94.1% (at 25°C) for outcrossed eggs (Costil, 1993). In *Lymnaea stagnalis appressa* Say, of a total of 4909 eggs from six isolated snails, 64.7% hatched (Cain, 1956). For *T. albolabris*, the percentages of offspring hatching as a result of outcrossing and of inbreeding were 73.2% and 2.7%, respectively (McCracken & Brussard, 1980). A lower percentage of hatching in self-fertilized eggs than in cross-fertilized eggs was also observed in *Physa gyrina* Say (De Witt, 1954). Such reductions in fertility would probably not allow the renewal of the population, which would disappear if self-fertilization were the sole mode of reproduction. Moreover, species occupying a wide diversity of habitats must have a higher amount of genetic variation, and this is better maintained with outcrossing than with selfing (Jarne et al., 1993). Lastly, inbred offspring produced by selfing have lowered fitness because an individual's genome will contain many deleterious, recessive alleles (McCracken & Brussard, 1980). These authors added that a parent should not invest resources in such offspring unless the probability of finding a mate is so low as to offset this reduced fitness.

According to Madsen et al. (1983), the American planorbid *Helisoma duryi* did not reproduce when the snails were isolated, but the opposite result has been reported by Paraense & Correa (1988). De Witt & Sloan (1959) reported that the sole capsule laid by an isolated individual of this species contained eggs which did not develop. It is possible that different populations belonging to the same species show differences in selfing ability (Paraense, 1993). This view appears to be supported by research on two populations of *Bulinus globosus*: in one population, self-fertilization could have been selected (value of self-fertilization depression, d , of 0.04), whereas in the other, the snails had a lower fitness when selfing than when outcrossing ($d = 0.39$) (Njiokou et al., 1992). The self-fertilization depression (Jarne et al., 1991) was estimated as $d = 1 - (W_s/W_c)$, with W_s and W_c , respectively, the fitness value for self-fertilization and cross-fertilization. Thus, the reproductive strategy adopted should be considered as an adaptive trait of the population to its environment and not a specific characteristic. According to Jarne

et al. (1993), the potential advantages of selfing over outcrossing include the nil cost of finding a mate and copulating (probably quite low) and the occurrence of locally adapted offspring. Moreover, this advantage particularly occurs in cases of low densities and parasitosis (for example, if parasites act negatively on the copulating behavior of snails). Aphilic snails do not develop a functional penis and prostate and can reproduce only by self-fertilization. In *Bulinus truncatus*, the proportions of aphilic and euphilic individuals produced depended on temperature which exerted an effect on eggs after deposition and on hatchlings but not on parental snails (Schrage & Read, 1992). When the population density is low (for example, when colonization occurs or after a disturbance event like drought which reduces density), the probability of finding a mate is low, and a snail's ability to produce offspring by self-fertilization is greatly favorable to the population survival. Compared with *P. corneus*, *P. planorbis* inhabits more temporary ponds (Klimowicz, 1959; Costil, 1993), so we might expect that the latter species would be more self-fertile than the first: in the present study, that is not the case. However, *P. planorbis* populations appear to be a little more dense than those of *P. corneus* (Costil, 1993), and *P. planorbis* has been reported to be especially drought-resistant (Matzke, 1959). In the latter species, allosperm could also be drought-resistant, as this has been reported in the genus *Bulinus* (Rudolph & Bailey, 1985) and in *B. glabrata* (Vianey-Liaud & Dussart, 1994). In such a case, an individual isolated after drought could restore a population if it had been cross-fertilized previously. Moreover, populations of *P. planorbis*, like populations of other freshwater snails, are generally connected with neighboring populations by means of floods, winds, animals (fishes, amphibia, cattle, and especially birds), and humans (Rees, 1965; Mouthon, 1980; Boag, 1986). Finally, snails have the capability of utilizing stored foreign sperm for a long period after copulation (Cain, 1956; Madsen et al., 1983; Rollinson & Wright, 1984; Vianey-Liaud, 1990), and such a mechanism must play an important part in conserving the gene pool of the species (Rollinson et al., 1989).

Self-fertility has been demonstrated in all basommatophoran species studied (Jarne et al., 1993). However, in the present study, *P. planorbis* does not seem to use self-fertilization, and *P. corneus* appears very reluctant to do so. These results demonstrate that the hermaphroditism of basommatophora does not necessarily imply self-fertilization in all species or in all populations of these species. The question of the mode of reproduction in the freshwater snails is complicated by the necessity to consider it in the environment of the snails. For example, it would be of great interest to know precisely what the selective forces are which direct snail populations toward cross- or self-fertilization at a given time of their life. One of the multiple issues raised by the mode of fertilization, and one which remains to be resolved, is to discover how the advantage of the foreign sperm over self sperm occurs.

ACKNOWLEDGMENTS

Thanks are due to Dr. M. Vianey-Liaud and M. A. Coultellec-Vreto for their useful comments on early drafts of this manuscript. We are deeply grateful to Pr. B. Bailey for checking the English.

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New Species of Middle Eocene Gastropods from the Northern Doty Hills, Southwestern Washington

by

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Abstract. Five new species of gastropods were found at three localities in pebbly mudstones in the transition zone of interbedded volcanic and sedimentary rocks between the upper part of the Crescent Formation and the overlying lower part of the McIntosh Formation, Lewis County, southwestern Washington. The depositional environment is interpreted to have been on the flank of an oceanic volcanic island in outer shelf to upper slope (bathyal) muds subject to the influx of shells of nearshore and shallow-marine megainvertebrates and pebbly basalt debris. Associated calcareous nannofossils and megafossils indicate assignment to the middle Eocene.

The fissurellid *Emarginula dotyhillensis* is the second Eocene species of this genus to be found on the Pacific coast of North America. The turbinid *Liotia washingtoniana* is the earliest record of this genus and only the second Eocene species to be found on the Pacific coast of North America. The trochid *Cidarina antiqua* is the first Paleogene species and the earliest record of this genus, whose previous geologic range was early Pleistocene to Recent. The trochid *Solariella* (*Solariella*) *garrardensis* is the third species of this genus to be found in Eocene rocks of Washington. The muricid *Pterynotus* (*Pterynotus*) *washingtonicus* is the second Eocene report of *Pterynotus* s.s. from the Pacific coast of North America.

INTRODUCTION

In the northern Doty Hills area, Lewis County, southwestern Washington (Figure 1), the junior author discovered abundant and well-preserved megafossils in Eocene rocks previously considered to be nearly barren of megafossils. Five new species of gastropods were found, and the objectives of this paper are to name and describe them and provide new information as to their stratigraphic position, geologic age, and general depositional environment.

The molluscan stages used in this report stem from Clark & Vokes (1936), who proposed five mollusk-based provincial Eocene stages, namely, "Meganos" (lowermost

Eocene), "Capay" (middle lower Eocene), "Domengine" (upper lower to lower middle Eocene), "Transition" (lower middle Eocene), and "Tejon" (middle middle Eocene to upper Eocene). The subseries equivalencies (shown in parentheses) of these stages are derived from Bartow (1992). The stage names are in quotes because they are informal terms and generally the same as formation names. Givens (1974) modified the use of the "Capay Stage," and it is in this modified sense that the "Capay Stage" is used herein. The calcareous nannofossil biozones follow that used by Okada & Bukry (1980). The classification system used for the turbinid and trochid gastropods follows that of Hickman & McLean (1990). Abbreviations used for catalog

and/or locality numbers are: CSUN, California State University, Northridge; LACMIP, Natural History Museum of Los Angeles County, Invertebrate Paleontology Section.

STRATIGRAPHY AND MEGAFaUNA

On the geologic map of Pease & Hoover (1957), the study area localities plot in the lower member of the McIntosh Formation. Pease & Hoover (1957) were the first to recognize lower and upper members of this formation and reported that the lower member consists of a sequence of interbedded sedimentary and volcanic rocks usually transitional with the underlying Crescent (?) Formation. In a sense, Pease & Hoover (1957) emended the definition of the McIntosh Formation, which originally referred (Snively et al., 1951) to chiefly dark gray, well-indurated tuffaceous marine siltstone and claystone interbedded with basaltic and arkosic sandstone in the lower part, and massive arkosic sandstone interbedded with andesite flows in the upper part. The type section of the McIntosh Formation is near Tenino, Washington, approximately 40 km northeast of the study area. According to early workers, invertebrate megafossils are rare in the McIntosh Formation and too poorly preserved for detailed study (Snively et al., 1951; Pease & Hoover, 1957; Snively et al., 1958). The only reference to a particular type of invertebrate megafossil was the report of unidentified "mud pectens" from the upper part of the McIntosh Formation (Pease & Hoover, 1957). The McIntosh Formation is gradationally overlain by or locally interbedded with the Northcraft and Skookumchuck Formations, and the latter formation is correlative to the upper middle Eocene (Armentrout et al., 1983).

The study area lithologies of thin lenses and pods of greenish pebbly mudstone, thin fossiliferous beds, muddy siltstone, and muddy sandstone, all interbedded with black basalt flows, are very similar to some lithologies in the upper Crescent Formation at the following locales: type section of the Crescent Formation west of Crescent Bay on the northern shore of the Olympic Peninsula (Arnold, 1906); Pulali Point on the east side of the Olympic Peninsula (Squires et al., 1992); and Little River area in the Satsop River drainage (Rau, 1966; Squires & Goedert, 1994a) (Figure 1). Because of these lithologic similarities, we believe that the upper Crescent Formation crops out in the study area and the use of a "question mark" by Pease & Hoover (1957) with the Crescent Formation in the northern Doty Hills is unnecessary. We believe also, pending detailed stratigraphic fieldwork, that the study area localities should be assigned to the transition zone of interbedded volcanic and sedimentary rocks present between the upper Crescent Formation and the overlying lower member of the McIntosh Formation (as used in the emended sense of Pease & Hoover, 1957).

The new species were found at three localities (CSUN locs. 1567, 1569, 1570, listed in ascending stratigraphic order) in a rock quarry where 17 m of section are exposed.



Figure 1

Index map to the northern Doty Hills, southwestern Washington.

The basal part, a 1 m-thick interval of siltstone and sandstone, is overlain by a 10 m-thick basalt unit that is blocky and fractured in the lower 7 m and brecciated in the upper 3 m. The lower contact of the 10-m thick basalt unit is baked, and the upper contact is erosional. There appears to have been paleo-relief in the area because the basalt flow crops out stratigraphically higher, relative to the quarry section, 100 m west of the quarry, and there is no evidence of faulting.

Overlying the basalt unit are 6 m of sedimentary rocks that include the three localities. The sedimentary strata in this 6 m-thick interval consist of fossiliferous siltstone interbedded with thin lenses and pods of pebbly mudstone, coarse sandstone, and minor amounts of coquina. Locality 1567 is near the top of a 20 cm-thick, greenish brown, poorly indurated pebbly mudstone bed that immediately overlies the 10 m-thick basalt unit. The rock clasts in the pebbly mudstone are subrounded and as large as 5 cm in length. The amount of mud increases upward in this bed, and locally there is laminated mudstone. Locality 1569 is 2 m stratigraphically above locality 1567 and consists of hard, platy grayish brown siltstone with scattered fossils. The siltstone locally encloses lenses of coquina, and they show normal graded bedding. Locality 1570, approxi-

mately 2 m upsection from locality 1569, is in a 2 m-thick brown sandstone bed with scattered lenses of basalt pebbles. At these three localities, the taxonomic composition of the macrofossils is similar (Table 1) and dominated by gastropods (including some minute specimens less than 5 mm in longest dimension) and bivalves. In addition, there can be megascopic benthic foraminifera (up to 2.8 mm in longest dimension), siliceous sponges, solitary corals, bryozoans, inarticulate and articulate brachiopods, polychaete tubes, scaphopods, a nautiloid, "gooseneck" barnacle opercula, crab chelipeds, isocrinid columnals, and shark teeth.

Fossils are abundant at all of the localities, and preservation of the fossils ranges from poor to good. The fossils are loosely packed and poorly sorted (terms used in the sense of Kidwell, 1991), except in the localized closely packed coquina lenses. Shells are not encrusted and rarely show any signs of boring. At all the localities, specimens of bryozoans and polychaetes are fragments. Specimens of the solitary coral *Flabellum clarki* Bentson are complete and have retained their delicate basal areas. The *Aphrocallistes polytretos* Rigby & Jenkins sponges are small fragments, but the *Eurete goederti* Rigby & Jenkins sponges are much larger fragments (up to 4 cm across). Brachiopods are usually unbroken single valves, but the bivalves are usually broken single valves, except for the unbroken *Parvamussium stanfordense* (Arnold), a small species. Some of the scaphopods are nearly complete. Gastropods are usually complete, especially *Solariella* (*Solariella*) *garrardensis* and *Cantrainea hieroglyphica* (Hickman). Many of the gastropods have retained their delicate morphologic features (e.g., protoconch, uppermost spire, sharp nodes, thin ribs, winged varices, long siphonal canal). Some of the "archaeogastropods" (including two of the new species) and some of the bivalves also have the mother-of-pearl luster of their interior shell layers preserved. The nautiloid has been crushed by sediment weight. The opercular plates of the barnacle *Aporolepas* sp. are unbroken. Most of the isocrinid columnals are disarticulated, although one specimen consists of an articulated columnal 1 cm in length.

AGE

The Crescent Formation, which can be as much as 16 km thick and is one of the thickest accumulations of volcanic rock in the world, ranges in age from the late Paleocene to the middle Eocene (Armentrout, 1987).

The McIntosh Formation transgresses time from middle to late Eocene and becomes younger in age toward the west from its type section east of the study area (Pease & Hoover, 1957). Armentrout et al. (1983), however, reported that the time transgressiveness of the McIntosh Formation encompasses only the middle Eocene. Just south of the Doty Hills area, the lower part of the McIntosh Formation was assigned by Rau (1958) to the upper part of Laiming's (1940) benthic foraminiferal Zone A-2, which is equivalent to the lower part of Mallory's (1959) benthic foraminiferal Narizian Stage. Almgren et al. (1988) recently emended Laiming's (1940) zones and correlated

most of Zone A-2 to the middle Eocene calcareous nannofossil Zone CP13 Zone of Okada & Bukry (1980). Relative to molluscan stages, Zone CP13 corresponds to the upper part of the "Domengine Stage," the "Transition Stage," and the lower part of the "Tejon Stage" (Bartow, 1992).

A poorly preserved but moderately diverse assemblage of calcareous nannofossils was found at CSUN locality 1567. Though classic zonal markers are absent, this sample can be assigned (M. V. Filewicz, personal communication) to the middle Eocene (Zones CP12 to CP14 of Okada & Bukry, 1980) based on the range overlap of *Chiasmolithus solitus* (Bramlette & Sullivan) and abundant large (>6 microns) *Reticulofenestra* spp., including *R. samudorovi* (Hay, Mohler & Wade). Bukry & Snively (1988) found a very similar calcareous nannofossil assemblage in a sedimentary and volcanic sequence of middle Eocene age just east of Dolph, northwestern Oregon. A microfossil sample from CSUN loc. 1570 is barren of nannofossils except for very rare *Reticulofenestra* spp. Unfortunately, the range of Zones CP12 to CP14 is quite broad and encompasses the "Domengine Stage," "Transition Stage," and part of the "Tejon Stage."

An analysis of the stage ranges of the identifiable species of megafossils in the study rocks (Table 1) shows that the megafossil data are not that conclusive and encompass the "Domengine," "Transition," and the "Tejon Stages." Although a few species (the solitary coral *Flabellum clarki* Bentson; the inarticulate brachiopod *Craniscus edwilsoni* Squires & Goedert; and the gastropod *Haplocochlias montis* Squires & Goedert) indicate the "Capay Stage," we do not assign the study area rocks to this stage because the fossil record of these species is incomplete. They are known only from single formations, and the gastropod *H. montis* is not commonly preserved because of its minute size. In addition, the nannofossil data put a constraint on the age of the study area rocks as younger than the "Capay Stage." Of all the other positively identified species listed in Table 1, only the gastropod *Homalopoma umpquaensis domingensis* Vokes does not have a geologic range that includes the "Transition" and "Tejon" "Stages." Its range is "Capay Stage" to "Domengine Stage," but this species is also relatively rare in the fossil record.

Although two species (the colonial coral *Dendrophyllia tejonensis* Nomland and the gastropod *Conus aegilops* Anderson & Hanna) seem to indicate the "Transition Stage," this is misleading because no molluscan species are known to be restricted to the short "Transition Stage" (Givens & Kennedy, 1979). The fossil record of these two species is incomplete, and both are known only from a single formation. Future work will undoubtedly show them to occur in more than just the "Transition Stage." Species listed in Table 1 that are more widespread and that have a moderately restrictive geologic age range are the gastropods *Patelloida tejonensis* (Gabb), *Pseudoperissolax blakei* (Conrad), and the bivalve *Brachidontes*? (*B.?*) *dichotomus* (Gabb), and they indicate the "Transition" to "Tejon" "Stages." Four other species listed in Table 1 (the articulate bra-

Table 1

Eocene megafossil taxa from the transition zone of interbedded volcanic and sedimentary rocks between the upper Crescent Formation and the overlying lower McIntosh Formation, northern Doty Hills, Washington. M = "Meganos Stage," C = "Capay Stage," D = "Domengine Stage," Tr = "Transition Stage," Te = "Tejon Stage."

Taxa	Localities & number of specimens				Previously reported stage range	Previously reported paleoenvironment; geologic range comments
	1567	1569	1570			
PORIFERA						
Hexactinellida						
<i>Aphrocallistes</i> sp. cf. <i>A. polytreto</i> s Rigby & Jenkins, 1963	1	—	—	Middle Eocene?, Te-Oligocene (Rigby & Jenkins, 1963; Goedert & Squires, 1990)	300–350 m (Rigby & Jenkins, 1983); chemosynthetic cold seeps (Goedert & Squires, 1990). Presence in Doty Hills is the earliest confirmed occurrence of this species.	
<i>Eurete goederti</i> ? Rigby & Jenkins, 1963	1	—	18	Oligocene (Rigby & Jenkins, 1963)	100–350 m (Rigby & Jenkins, 1983). Presence in Doty Hills is the earliest occurrence of this species.	
CNIDARIA						
Anthozoa						
<i>Dendrophyllia tejonensis</i> Nomland, 1916	4	—	3	Tr (Squires, 1989a; Lindberg & Squires, 1990)	Rocky nearshore, reported only from basal Tejon Formation, southern California (Squires, 1989a; Lindberg & Squires, 1990).	
<i>Flabellum clarki</i> Benton, 1943	3	3	6	C (Benton, 1943)	Marine, reported only from Capay Fm., northern California (Benton, 1943).	
BRYOZOA						
Unidentified encrusting bryozoan	2	—	—	—	—	
Unidentified frond-like bryozoan	2	—	1	—	—	
BRACHIOPODA						
Inarticulata						
<i>Craniscus edwilsoni</i> Squires & Goedert, 1994	1	—	—	C (Squires & Goedert, 1994a)	Hard substrate associated with volcanic island or pillow basalt in shallow-marine waters, reported only from upper part of Crescent Fm., Washington (Squires & Goedert, 1994a).	
<i>Terebratulina washingtonensis</i> (Weaver, 1912)	—	25	4	Te	Marine, reported only from Cowlitz Fm., Washington (Weaver, 1912). Armentrout et al. (1983) assigned formation to the upper Eocene.	
ANNELIDA						
Polychaeta						
<i>Rotularia (Rotularia) tejonense</i> (Arnold, 1910)	1	—	—	C-Tr (Squires & Goedert, 1994a)	Subtidal in rubble derived from closely adjacent basalt flows extruded into shallow-marine waters, and hard substrate associated with volcanic island or pillow basalt in shallow-marine waters (Squires et al., 1992; Squires & Goedert, 1994a).	

Table 1
Continued.

Taxa	Localities & number of specimens			Previously reported stage range	Previously reported paleoenvironment; geologic range comments
	1567	1569	1570		
<i>Rotularia</i> sp. (smooth)	—	3	6	—	—
MOLLUSCA					
Scaphopoda					
<i>Dentalium</i> sp. (ribbed)	—	6	2	—	—
<i>Dentalium</i> sp. 2 (smooth)	1	3	5	—	—
Gastropoda					
<i>Cantrainea hieroglyphica</i> (Hickman, 1974)	2	54	5	Te	Outer shelf to upper slope (bathyal), reported only from upper Cowlitz Formation, northern Oregon (Hickman, 1974). Armentrout et al. (1983) assigned this formation to the upper middle Eocene.
<i>Cidarina antiqua</i> sp. nov.	—	1	10	—	Previously, genus only known as Recent.
<i>Conus aegilops</i> Anderson & Hanna, 1925	1	10	2	Tr	Only known from Liveoak Shale Members of the Tejon Formation (unpublished data). Nil- sen (1987) and Squires (1989b) assigned this member to the "Transition Stage." Nilsen (1987) assigned this member to the deep ma- rine (bathyal).
<i>Cypraea gemmula warnerae</i> Effinger, 1938	3	—	2	Te	Interbedded nearshore or littoral facies and slightly deeper (not over 60 to 90 m in depth) facies, reported only from Gries Ranch beds, Washington (Effinger, 1938). Lindberg (1988) assigned the Gries Ranch beds to the upper Eocene.
<i>Cyclchnina tantilla</i> (Anderson & Hanna, 1925)	—	—	2	C-Te (Squires & Demetron, 1992)	Subtidal, in rubble derived from closely adjacent basalt flows extruded into shallow-marine wa- ters (Squires et al., 1992). Shallow marine (Squires & Demetron, 1992).
<i>Emarginula dotyhillensis</i> sp. nov.	—	—	3	—	—
<i>Erginus vaderensis</i> (Lindberg, 1979)	2	—	3	C-Te (Squires & Goedert, 1994a)	Hard substrate associated with volcanic-island or pillow basalt in shallow-marine waters (Squires & Goedert, 1994a).
<i>Gemmula abacta</i> Anderson & Hanna, 1925	—	—	1	Eocene undifferentiated (Anderson & Hanna, 1925)	Tejon Formation (Anderson & Hanna, 1925).
<i>Gemmula barksdalei</i> ? Weaver, 1942	—	—	1	Te	Cowlitz Formation, Washington (Weaver, 1912). Armentrout et al. (1983) assigned this forma- tion to the upper middle Eocene. Also found near base of Mettralla Sandstone in Liveoak Canyon, Tehachapi Mountains, southern Cal-

Table 1
Continued.

Taxa	Localities & number of specimens			Previously reported stage range	Previously reported paleoenvironment; geologic range comments
	1567	1569	1570		
<i>Haplocochlias montis</i> Squires & Goedert, 1994b	5	1	—	C (Squires & Goedert, 1994a)	ifornia (unpublished data). Nilsen (1987) assigned this formation to the "Tejon Stage" and assigned this formation in Liveoak Canyon to the shallow-marine environment. Rocky intertidal, reported only from upper part of Crescent Formation, Washington (Squires & Goedert, 1994a).
<i>Hipponix arnoldi</i> Dickerson, 1917	—	—	3	Te	Interbedded nearshore or littoral facies and slightly deeper (not over 60 to 90 m in depth) facies, reported only from Gries Ranch beds of the late Eocene age (Effinger, 1938). Lindberg (1988) assigned the Gries Ranch beds to the upper Eocene. Transition zone between protected rocky shoreline and offshore (Squires, 1988a).
<i>Homalopoma umpquaensis domenginensis</i> Vokes, 1939	1	—	2	C-D (Squires, 1988a)	—
<i>Liotia washingtoniana</i> sp. nov.	2	—	—	—	Rocky nearshore (Lindberg & Squires, 1990).
<i>Patelloida tejonensis</i> (Gabb, 1869)	—	—	1	Tr-Te (Lindberg & Squires, 1990)	—
<i>Polinices</i> (<i>Polinices</i>) <i>hornii</i> (Gabb, 1864)	1	—	3	Upper Paleocene-Te (Marincovich, 1977)	Most abundant in upper Eocene rocks (Marincovich, 1977).
<i>Pseudoperissolax blakei</i> (Conrad, 1855)	—	—	1	Tr-Te (Givens & Kennedy, 1979; Nilsen, 1987)	Inner neritic on rocky substrate and shallow marine (Nilsen, 1987). Presence in Doty Hills is first occurrence in Washington.
<i>Pterynotus</i> (<i>Pterynotus</i>) <i>washingtonicus</i> sp. nov.	—	—	2	—	—
<i>Solariella</i> (<i>Solariella</i>) <i>garrardensis</i> sp. nov.	3	—	53	—	—
<i>Turritella</i> sp. indet.	1	—	—	—	—
Bivalvia	—	—	—	—	—
<i>Acila</i> sp. indet.	—	2	—	—	—
<i>Brachidontes</i> (<i>Brachidontes</i>) <i>cowlitzensis</i> Weaver and Palmer, 1992	2	—	—	Me-lower Oligocene (Squires & Goedert, 1994a)	Hard substrate associated with volcanic island or pillow basalt in shallow-marine waters (Squires & Goedert, 1994a).
<i>Brachidontes</i> ? (<i>Brachidontes</i> ?) <i>dichotomus</i> (Gabb, 1864)	3	—	3	Tr-Te (Weaver, 1912; Lindberg & Squires, 1990)	Rocky nearshore (Lindberg & Squires, 1990).
<i>Chama</i> sp.	1	—	—	—	—
" <i>Crassatella</i> " <i>wasana</i> Conrad, 1855	—	—	2	D-Te (Squires, 1987)	Shallow marine (Squires, 1984) and transition zone just seaward of a delta front (Squires, 1987).
<i>Glycymeris</i> sp.	5	—	9	—	—
<i>Isoognomon</i> (<i>Isoognomon</i>) <i>clarki</i> (Effinger, 1938)	1	—	—	D-Te (Squires, 1989a)	Rocky nearshore to possibly bathyal (Squires, 1989a).

Table 1
Continued.

Taxa	Localities & number of specimens				Previously reported stage range	Previously reported paleoenvironment; geologic range comments
	1567	1569	1570			
<i>Nemocardium linteum</i> (Conrad, 1855)	—	—	3	Upper Paleocene-Te (Squires & Goedert, 1994a)	Shallow marine (Squires, 1984); subtidal in rubble derived from closely adjacent basalt flow extruded into shallow marine waters (Squires et al., 1992); and offshore (Squires & Demettrion, 1992)	
<i>Ostrea</i> sp.	1	—	3	—	—	
<i>Parvamussium stanfordense</i> (Arnold, 1906)	—	—	10	C-Te (Moore, 1984)	Presence in Doty Hills is first occurrence in Washington. "Capay Stage" occurrence not given <i>per se</i> by Moore (1984) but a specimen (pl. 1, fig. 15) is reported by her from the Cerros Shale Member of the Lodo Formation, central California. See Squires (1988b) for a discussion of the age of this member.	
<i>Pleria</i> sp., cf. <i>P. clarki</i> Weaver & Palmer, 1922	—	—	1	Te	Cowlitz Formation, Washington (Weaver & Palmer, 1922). Armentrout et al. (1980) assigned this formation to the upper middle Eocene.	
<i>Spondylus carlosensis</i> Anderson, 1905	1	—	—	C-Te (Weaver & Kleinpell, 1963; Squires & Goedert, 1994a).	Hard substrate associated with volcanic island or pillow basalt in shallow-marine waters (Squires & Goedert, 1994a).	
Cephalopoda	—	1	—	—	—	
Unidentifiable nautiloid	—	—	—	—	—	
ARTHROPODA	—	—	—	—	—	
Cirripedia	15	—	4	—	—	
<i>Aporolepas</i> sp. (opercular plates)	—	—	—	—	—	
Brachyura	—	4	—	—	—	
Crab chelipeds	—	—	—	—	—	
ECHINODERMATA	—	—	—	—	—	
Crinoidea	1	—	4	—	—	
Isocrinid (columnals)	—	—	—	—	—	
CHORDATA	—	—	—	—	—	
Chondrichthyes	—	—	—	—	—	
<i>Notorhynchus</i> ? sp. (tooth)	—	1	—	—	—	
Known species are from a subtidal/inner shelf agitated environment (R. T. Perreault, personal communication).	—	—	—	—	—	

chiopod *Terebratulina washingtoniana* (Weaver), and the gastropods *Cantrainea hieroglyphica* (Hickman), *Cypraea gemmula warnerae* Effinger, and *Hipponix arnoldi* Dickerson, indicate the "Tejon Stage," but the reported stage ranges of these species are suspect because the species are known only from a single formation. The same reasoning holds for the sponge *Eurete goederti* Rigby & Jenkins listed in Table 1.

In summary, the megafossil data are not useful in assigning the study area rocks to any one molluscan stage with certainty. Based on Rau's (1958) work on the age of the formation, as well as on the constraint of the nannofossil data at locality 1567, and considering that megafossils with the best fossil record indicate the "Transition Stage" to "Tejon Stage," the latter of which is mostly of middle Eocene age, we conclude that the study area rocks should be generally assigned to the middle Eocene.

GENERAL DEPOSITIONAL ENVIRONMENT

Taken as a whole, the Crescent Formation accumulated in a subsiding basin that was formed by rifting along the continental margin of Washington and Oregon, and volcanic islands developed where extrusion exceeded the rate of basin subsidence (Babcock et al., 1992, 1994). The upper third of the formation ranges from a deep-to-shallow marine environment to one that is locally terrestrial. Where extrusion of basalt flows caused shoaling of the marine waters, interbedded marine sedimentary rocks locally contain megafossils (Squires et al., 1992; Squires & Goedert, 1994a; Squires & Goedert, 1994b).

The lower part of the McIntosh Formation includes nearshore sequences of basaltic and arkosic sandstone that grade toward the west into offshore deep-water siltstone and claystone that make up the middle part of the formation (Armentrout, 1987).

An analysis of the paleoenvironments that have been previously reported for the identifiable species found in the study area rocks (Table 1) shows that most of the paleoenvironments are nearshore to shallow-subtidal and contain rubble derived from closely adjacent rocky shores usually made up of basalt flows. The paleoenvironments for the siliceous sponges and the gastropods *Cantrainea hieroglyphica* and *Conus aegilops*, however, are outer shelf to upper slope (bathyal). The close association of a nearshore paleoenvironment with an outer shelf paleoenvironment for the study area rocks is compatible with the above-mentioned depositional history of the upper part of the Crescent Formation, as well as with the depositional history of the lower part of the McIntosh Formation.

In terms of lithologies, the Doty Hills study area rocks are most similar to the upper Crescent Formation at Pulali Point on the east side of the Olympic Peninsula, Washington, where muddy pebble conglomerates were deposited in a shallow-subtidal environment next to basalt flows that had caused shoaling of the marine waters (Squires et al., 1992). The similarities are the following: muddy pebbly bed immediately overlies a basalt flow, pebble clasts are

subrounded and consist of basalt, muddy pebbly bed grades upward into thicker intervals of siltstone or mudstone, and megafossil groups are dominated by gastropods and bivalves in association with bryozoans, brachiopods, scaphopods, and nautiloids.

In terms of taxonomic composition, the Doty Hills study area rocks are most similar to the upper Crescent Formation in the Little River area on the south side of the Olympic Peninsula, Washington, where a diverse assemblage of megainvertebrates lived on a hard substrate produced by the accumulation of bouldery rubble derived from volcanic-island or pillow basalt in shallow-marine waters (Squires & Goedert, 1994a). Species found in the Doty Hills study area that are conspecific with those in the Little River area are: *Craniscus edwilsoni* Squires & Goedert, *Rotularia* (R.) *tejonense* (Arnold), *Erginus vaderensis* (Dickerson), *Brachidontes* (B.) *cowlitzensis* Weaver & Palmer, *Spondylus carlosensis* Anderson, and *Nemocardium linetum* (Conrad). In addition, the barnacle *Aporolepas* sp. is present at both sites.

The depositional environment of the sedimentary rocks in the study area is interpreted to have been on the flank of an oceanic volcanic island in outer shelf to upper slope (bathyal) muds and silts subject to the influx, during storms, of shells of nearshore and shallow-marine megainvertebrates and pebbly basalt debris. On the flank of a volcanic island, the distance of downslope transport would not have been necessarily great to reach upper bathyal depths. There was minimum duration of seafloor exposure because the shells do not show evidence of borers, encrusters, or crushers, which are normally associated with delayed burial (Kidwell, 1991). Species indigenous to this outer shelf to upper slope environment were the siliceous sponges and the gastropods *Cantrainea hieroglyphica* and *Conus aegilops*. A detailed paleoecologic/taphonomic study is needed to determine which of the other species are indigenous or exotic to the site of accumulation, but such a study is beyond the scope of the present report.

SYSTEMATIC PALEONTOLOGY

Class Gastropoda Cuvier, 1797

Family FISSURELLIDAE Fleming, 1822

Subfamily EMARGINULINAE Gray, 1834

Genus *Emarginula* Lamarck, 1801

Type species: *Emarginula conica* Lamarck, 1801, by original designation, Miocene to Recent, living in Finland and coasts of Great Britain to the Adriatic Sea (Palmer, 1937).

Emarginula dotyhillensis

Squires & Goedert, sp. nov.

(Figures 2–4)

Diagnosis: An *Emarginula* with apex near posterior margin, moderately long anal slit, 16 primary radial ribs with two main rows of nodes (diverging and coarsening ante-

riorly), and double or single row of punctations between ribs.

Description: Shell small, sturdy, with nearly parallel sides. Apex strongly curved posteriorly and directly above posterior margin. Anterior slope convex and steep near anterior margin; posterior slope concave below the apex. Apex smooth, nucleus turned under the succeeding part of shell. Anal slit situated at anterior margin, narrow and moderately deep, measuring 0.75 mm deep. Slit band coincident with raised area extending nearly to apex. Sculpture of 16 strong primary radial ribs originating near apex. Interspaces between primary radial ribs with double rows of punctations on anterior and posterior slopes; single row (less commonly, double rows) of punctations on lateral slopes. Concentric sculpture consists of two raised ridges, noded at intersections with the primary radial ribs on lower part of shell; nodes diverge and coarsen anteriorly; a third row nodes only near the slit band. Aperture ovate.

Dimensions of holotype: Length 3.4 mm, width 2.6 mm, height 3 mm.

Holotype: LACMIP 12338.

Type locality: CSUN loc. 1570, latitude 46°45'52"N, longitude 123°19'00"W.

Discussion: Only a single specimen was found, but it is complete and well-preserved. The new species is similar to *Emarginula fenestrata* Deshayes (1864–1866:350, pl. 3, figs. 37–41; Cossmann & Pissarro, 1910–1913:pl. 2, fig. 10-1; from the middle Eocene (Lutetian Stage) of the Paris Basin, France. The new species differs in the following features: no secondary radial ribs, concentric ribs only on lower part of shell rather than covering the shell, apex more posteriorly located, deeper anal slit, and presence of nodes on lower part of shell.

Emarginula dotyhillensis is only the second Cenozoic species of this genus to be reported from the Pacific coast of North America. The other species is *Emarginula washingtoniana* Squires & Goedert, 1994b from "Capay Stage"

rocks in the upper Crescent Formation at Larch Mountain, Black Hills, southwestern Washington (Squires & Goedert, 1994b). *Emarginula dotyhillensis* differs from *E. washingtoniana* in the following features: no secondary radial ribs, apex more posteriorly located, presence of nodes on lower part of shell, and presence of rows of punctations between the primary radial ribs.

Etymology: The new species is named for the Doty Hills, Washington.

Family TURBINIDAE Rafinesque, 1815

Subfamily LIOTIINAE Adams & Adams, 1854

Genus *Liotia* Gray, 1847

Type species: *Delphinula cancellata* Gray, 1828, by monotypy, Recent, northern Chile.

Liotia washingtoniana
Squires & Goedert, sp. nov.

(Figures 5–8)

Diagnosis: A species of *Liotia* with many closely spaced axial ribs on body whorl.

Description: Minute shell, three whorls. Very low spire but not flattened. Moderately strong cancellate sculpture, body whorl tabulate with three equal spiral ribs between shoulder and base of whorl, four additional ribs on base. Approximately 21 closely spaced axial ribs on body whorl; axial ribs extend from suture to narrow umbilicus. Aperture round. Shell interior nacreous.

Dimensions of holotype: Height 1.5 mm, diameter 2.5 mm.

Holotype: LACMIP 12339.

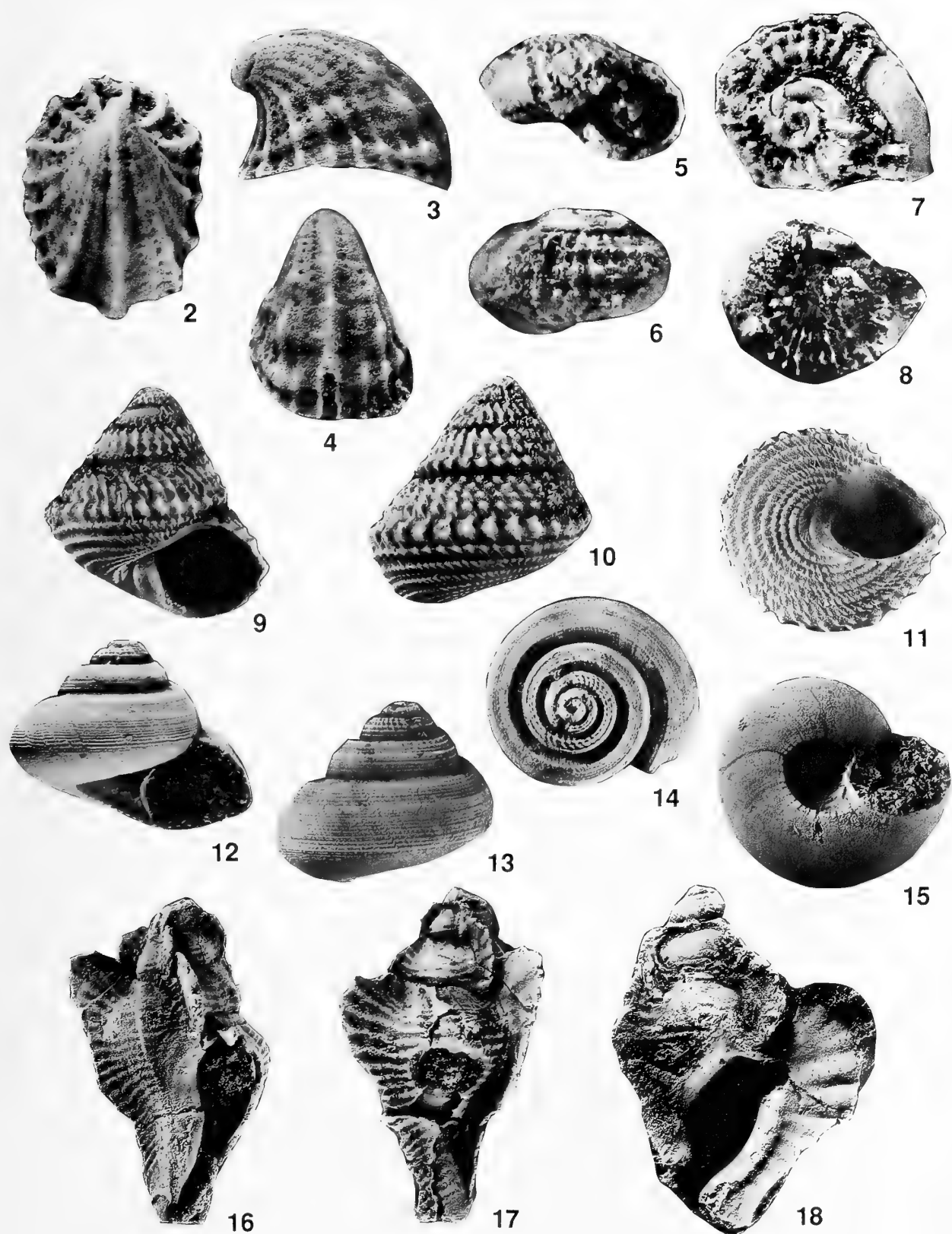
Type locality: CSUN loc. 1567, latitude 46°45'52"N, longitude 123°19'00"W.

Explanation of Figures 2 to 18

All specimens coated with ammonium chloride; photographed by the senior author. All specimens from CSUN loc. 1570, unless otherwise noted.

Figures 2–4. *Emarginula dotyhillensis* Squires & Goedert, sp. nov., holotype LACMIP 12338. Figure 2: dorsal view, $\times 12$, length 3.4 mm. Figure 3: left-lateral view, $\times 10$, height 3 mm. Figure 4: anterior view, $\times 11$, width 2.6 mm. Figures 5–8. *Liotia washingtoniana* Squires & Goedert, sp. nov., holotype LACMIP 12339, CSUN loc. 1567. Figure 5: apertural view, $\times 14$, height 5 mm. Figure 6: abapertural view, $\times 14$, height 6 mm. Figure 7: apical view, $\times 15$, diameter 2.5 mm. Figure 8: umbilical view, $\times 14$, diameter 2.5 mm. Figures 9–11. *Cidarina antiqua* Squires

& Goedert, sp. nov., holotype LACMIP 12340. Figure 9: apertural view, $\times 5.6$, height 7.1 mm. Figure 10: abapertural view, $\times 5.6$, height 7.1 mm. Figure 11: umbilical view, $\times 5.6$, width 7 mm. Figures 12–15. *Solariella* (Solariella) *garrardensis* Squires & Goedert, sp. nov. Figure 12: holotype LACMIP 12343, $\times 5.3$, height 6.2 mm. Figures 13–14: paratype LACMIP 12344. Figure 13: abapertural view, $\times 6.9$, height 4.4 mm. Figure 14: apical view, $\times 6.9$, width 5.3 mm. Figure 15: holotype LACMIP 12343, umbilical view, $\times 5$, width 7.4 mm. Figures 16–18. *Pterynotus* (*Pterynotus*) *washingtonicus* Squires & Goedert, sp. nov., Figures 16–17: holotype LACMIP 12351. Figure 16: apertural view, $\times 3.2$, height 17.5 mm. Figure 17: abapertural view, $\times 3.3$, height 17.5 mm. Figure 18: paratype LACMIP 12352, apertural view, $\times 6.8$, height 18.8 mm.



Discussion: Only two specimens were found; one is very poorly preserved.

There are two living species of *Liotia*, one from California and northern Baja California, and one from northern Chile. The new species is most similar to the living species *L. fenestrata* Carpenter, 1864, which has been illustrated by Palmer (1958:pl. 19, figs. 10, 11), McLean (1978:fig. 7), and Hickman & McLean (1990:fig. 8c). *Liotia fenestrata*, which is known from Monterey Bay, California, to San Martin Island, northern Baja California (Palmer, 1958), is also known as a rare fossil in the lower Pleistocene Lomita Marl of southern California (Woodring et al., 1946). The new species differs from *L. fenestrata* by having weaker cancellate sculpture and more closely spaced ribs.

The only other known fossil species of this genus is *L. weaveri* Effinger (1938:374–375, pl. 46, figs. 15, 21; Weaver, 1942 [1943]:pl. 63, figs. 13, 18) from the “Gries Ranch beds” of southwestern Washington. Lindberg (1988) assigned these beds to the upper Eocene part of the Lincoln Creek Formation. The new species differs from *L. weaveri* by having a spire that is not flattened, less prominent ribs, equal-strength ribs, 21 rather than 16 axial ribs, much narrower umbilicus, and aperture circular in outline rather than subhexagonal.

Previously, the geologic range of genus *Liotia* was late Eocene to Recent, but the discovery of the new species changes this range to early middle Eocene to Recent.

Etymology: The species is named for the state of Washington.

Family TROCHIDAE Rafinesque, 1815

Subfamily EUCYCLINAE Koken, 1897

Genus *Cidarina* Dall, 1909

Type species: *Margarita cidaris* A. Adams in Carpenter, 1864, by original designation, Pleistocene to Recent, living in Alaska to northern Baja California, Mexico.

Cidarina antiqua Squires & Goedert, sp. nov.

(Figures 9–11)

Diagnosis: A small-shelled species of *Cidarina* with a sharp medial angulation on body whorl and equal strength, closely spaced spiral ribs on spire.

Description: Shell small, five to six whorls. Suture impressed, channeled. Spire elevated, spire whorls flattened. Body whorl overall rounded but with a medial angulation. Surface covered by nodose spiral ribs: three on upper spire whorls, three to five on penultimate whorl and posterior half of body whorl, and seven on base of body whorl. Strongest spiral rib on angle on body whorl. Spirals on base of body whorl weaker than the others and nodes more beadlike. Upper spire whorls with cancellate ornamentation. Remaining whorls, especially base of body whorl,

with prominent prosocline growth lines. Aperture circular. Outer lip thin. Inner lip and columella with a callus that closes the umbilicus. Shell interior nacreous.

Dimensions of holotype: Height 7.1 mm, width 7.0 mm.

Holotype: LACMIP 12340.

Type locality: CSUN loc. 1570, latitude 46°45'52"N, longitude 123°19'00"W.

Paratypes: LACMIP 12341 and 12342.

Discussion: Eleven specimens of the new species were found, and almost all are from CSUN loc. 1570. They range in height from 2.5 to 10 mm. Seven of the specimens are complete, and only the largest specimen is abraded. A single specimen was found at CSUN loc. 1569.

Previously, *Cidarina* was known to be a monotypic genus represented by the extant *C. cidaris*. *Cidarina cidaris*, which is known from Kasañ Bay, Alaska to Cape San Quintin, northern Baja California (Dall, 1909), has a geologic range extending back to the early Pleistocene. Most of the Pleistocene records are in southern California, but one is known for the Pleistocene of Monterey Bay, central California, and one is known for the Pleistocene of northern Baja California (Arnold, 1903; Grant & Gale, 1931; Woodring et al., 1946; Powell, 1994). Arnold's (1903) so-called Pliocene specimens are early Pleistocene in age (Woodring et al., 1946). Dall (1909) reported *C. cidaris* from “deep waters” but gave no depth range. Hickman & McLean (1990:fig. 44G) illustrated a specimen collected at a depth of 27 m off Santa Catalina Island, southern California. The new species is similar but differs from *C. cidaris* by smaller size, sharper medial angulation on the body whorl, uniform strength of spiral ribs posterior to the medial angulation rather than alternating weak and strong ribs, and more closely spaced spiral ribs on the spire.

The new species is the first reported Paleogene species of *Cidarina* and the earliest record of this genus.

Etymology: The specific name is derived from *antiquus*, Latin, meaning old or ancient.

Subfamily SOLARIELLINAE Powell, 1951

Genus *Solariella* Wood, 1842

Type species: *Solariella maculata* Wood, 1842, by monotypy, Pliocene, England.

Subgenus *Solariella* s.s.

Solariella (*Solariella*) *garrardensis*
Squires & Goedert, sp. nov.

(Figures 12–15)

Diagnosis: A species of *Solariella* (*Solariella*) with tabulate whorls, bicarinate spire whorls, tricarinate body whorl, whorls covered by numerous very fine spiral ribs, cancellate upper spire whorls, and smoothish body whorl base.

Description: Small, up to 10 mm high, six to seven convex whorls. Suture distinct. Spire elevated, about one-half of shell. Body whorl moderately expanding. Protoconch smooth. Spire whorls and body whorl bicarinate with tabulate shoulder and medial angulation. On shells larger than about 8 mm height, medial angulation obsolete. Base of body also delineated by an angulation. Upper spire whorls cancellate, with axial ribs continuing across tabulate shoulder to suture. Remaining portion of spire and body whorl covered only with numerous, closely spaced, very fine spiral ribs. Spiral ribs obsolete to nearly obsolete on nearly smooth base of whorl. Growth lines prosocline. Umbilicus moderately wide and deep, umbilical shoulder delineated by a low row of numerous nodes. Interior of umbilicus smooth. Aperture quadrate, discontinuous. Shell interior nacreous.

Dimensions of holotype: Height 6.2 mm, width 7.4 mm.

Holotype: LACMIP 12343.

Type locality: CSUN loc. 1570, latitude 46°45'52"N, longitude 123°19'00"W.

Paratypes: LACMIP 12344 to 12350.

Discussion: Fifty-three specimens were found at CSUN loc. 1570, and three were found at CSUN loc. 1567. They are mostly complete and unabraded. At CSUN loc. 1570 they range in height from 2 to 7 mm and form a partial growth series.

The new species is similar to *Solariella olequahensis* Weaver & Palmer (1922:27–28, pl. 12, figs. 10, 12; Weaver, 1942 [1943]:293, pl. 64, figs. 6, 9) from the upper middle Eocene Cowlitz Formation, southwestern Washington. The new species differs in the following features: larger (up to 7 mm height rather than only 4 mm), whorls more tabulate, spiral ribs finer and not beaded or scalelike, spiral ribs much more numerous on body whorl, body whorl tricarinate rather than bicarinate, body whorl base not as sharply angulate, and spiral ribs on body whorl base tend to be obsolete.

There are only two other known species of Eocene *Solariella* from the Pacific Northwest. One is *S. crescentensis* Weaver & Palmer (1922:28–29, pl. 12, fig. 11; Weaver, 1942 [1943]:293–294, pl. 63, fig. 27) from the upper Crescent Formation on the north side of the Olympic Peninsula, Washington. The new species differs by not having well-defined beaded spiral ribs on the base of the body whorl. The other known species is *S. cicca* Hickman (1980:21–22, pl. 2, figs. 13, 14) from the upper Eocene Keasey Formation, northwestern Oregon, and in coeval strata on the Willapa River at Holcomb, Washington. The new species differs by having a lower spire, a wider umbilicus, a more pronounced and flatter spire, fewer and weaker spiral ribs on the body whorl, and no faintly cancellate pattern on the body whorl.

There are six other known species of *Solariella* from the Paleogene of the west coast of North America, and these

species are listed in Keen & Bentson (1944). Two of these species are Paleocene in age, and the others are Eocene. The one that is most similar to the new species is *S. hartleyensis* Clark & Woodford (1927:122–123, pl. 22, fig. 12) from lowermost Eocene ("Meganos Stage") strata near San Francisco, northern California. Although the apex of *S. hartleyensis* is not known, the new species differs by more tabulate body whorls, no sutural collar, more spiral ribs, no alternating strength of spiral ribs, and a more convex base.

Etymology: The new species is named for Garrard Creek, which is just east of the type locality.

Family MURICIDAE Rafinesque, 1815

Subfamily MURICINAE Rafinesque, 1815

Genus *Pterynotus* Swainson, 1833

Type species: *Murex pinnatus* Swainson, 1822, by subsequent designation, Swainson, 1833, Recent, western Pacific and eastern Indian Ocean.

Subgenus *Pterynotus* s.s.

Pterynotus (*Pterynotus*) *washingtonicus*
Squires & Goedert, sp. nov.

(Figures 16–18)

Diagnosis: A *Pterynotus* s.s. with prominent spiral ribs, one intervarical noded axial rib, and very weak denticles on the outer lip.

Description: Small shell, about six convex whorls. Suture distinct. Fusiform with a moderately high spire. Protoconch and uppermost spire missing. Shell bears three wing-like varices, each extending along siphonal canal to upper spire and, presumably, to apex. Each wing broadest in its shoulder portion. Wings continuous but undulating, with each recurved and overlapping in its uppermost portion to the corresponding varical wing of the preceding whorl. Other axial sculpture consists of a low ridge, nodose at shoulder, in each intervarical space. Spiral sculpture consists of about 20 spiral cords, more closely spaced and finer near the suture. Ornament of spiral cords continues onto both sides of the wings, with the spiral cords on the leading sides (apertural sides) of wings, especially at broadest points, weaker or even obsolete. Aperture narrow, outer lip erect and very faintly dentate with at least six denticles. Inner lip callused and smooth. Siphonal canal open. Growth lines well developed near suture and more strongly prosocline than elsewhere.

Dimensions of holotype: Height 17.5 mm, width 10.0 mm.

Holotype: LACMIP 12351.

Type locality: CSUN loc. 1570, latitude 46°45'52"N, longitude 123°19'00"W.

Paratype: LACMIP 12352.

Discussion: Only two specimens were found, and both are from CSUN loc. 1570. They range in height from 17.5 to 18.6 mm. Preservation is moderately good, but the uppermost spire and anteriormost portions of the shell are missing, as well as portions of the delicate varical wings. Only the paratype shows the outer lip, but the anterior part is missing. The portion of the outer lip that is present has very low denticles that do not photograph well.

The new species is assigned to *Pterynotus* s.s. because of the following: three varices that project beyond the varical rib into a flange or winglike blade, ovate aperture, open siphonal canal, spiral ornamentation on the varical wings, and dentate outer lip. Muricine taxa with trivariate winged shells that, on teleoconch characters, closely resemble *Pterynotus* s.s. are *Purpurellus* Jousseaume, 1880, *Pteropurpura* Jousseaume, 1880, and *Pterochelus* Jousseaume, 1880. *Purpurellus* is distinguished by a round aperture and a sealed siphonal canal with the left margin overlapping the right. *Pteropurpura* is distinguished by a round aperture and a fused siphonal canal (or at least the posterior two-thirds). *Pterochelus* is distinguished by having a varical wing that ends at the shoulder in a spine with a well-developed median channel.

The new species is very similar to *Pterynotus* (*Pterynotus*) *flemingi* Beu (1967:102, pl. 1, fig 9; 1970:138–141, pl. 2, figs. 16–17, 19–26) from the late Pliocene to Recent in New Zealand. This New Zealand species was originally deemed by Beu (1967) to be a subspecies of *P. (P.) laetifica* and assignable to genus *Pterynotus* s.s. Although Beu (1970) reassigned the subspecies to genus *Pteropurpura*, Beu & Maxwell (1990) put *laetifica* and *flemingi* back in genus *Pterynotus* s.s. and elevated *flemingi* to the species level. *Pterynotus* (*Pterynotus*) *washingtonicus* differs from *Pterynotus* (*Pterynotus*) *flemingi* in the following features: smaller shell, narrower spire, narrower aperture, weaker denticles on outer lip, and no tendency for outer lip to be scaly. That the new species is very similar to the living *P. (P.) flemingi* is not surprising because *Pterynotus* is a very conservative group, and there has been little morphological change in this line since the Paleocene (Vokes, 1970, 1971a). Harasewych & Jensen (1979) also reported very close similarity between a Paleocene species and a Recent species of *Pterynotus* s.s.

The new species is similar to *Murex trigonus* Roualt (1850:493, pl. 17, figs. 17–17a) from the lower Eocene (Ypresian Stage) near Pau in southern France. Roualt's species is preoccupied by *Murex trigonus* Gmelin, 1791. The new species differs in the following features: presence of an axial ridge in each intervarical space, absence of cancellate sculpture, much weaker denticles on the outer lip, and varices not scaly.

The new species resembles *Pterynotus crenulatus* (Röding, 1798) from the middle and upper Eocene (Lutetian and Bartonian Stages) of the Anglo-Paris Basin, France. Wrigley (1930), Vokes (1971b, 1992), and Le Renard

(1992) have given discussions or comments regarding the rather involved nomenclatural history of *P. crenulatus*. Illustrations of *P. crenulatus*, under the name of *Murex tricarlinatus* Lamarck, 1803, are given in Palmer (1977:pl. 4, figs. 7a, 7b) and in Cossman & Pissarro (1910–1913:pl. 35, fig. 169–5). The new species differs from *P. crenulatus* in the following features: intervarical spiral sculpture more pronounced, 20 rather than about nine spiral cords, no hint of a channel in the posterior portion of the winged varix on the outer lip, and much weaker denticles on the outer lip.

The new species also resembles *Pterynotus* (*Pterynotus*) *sabinola* (Palmer, 1937:266, pl. 36, figs. 7, 11, 12; Vokes, 1970:9–10, pl. 1, figs. 2a, 2b; Vokes, 1992:9, pl. 1, fig. 5) from the middle Eocene of Texas and Louisiana. The new species differs in the following features: more flared varices, spiral sculpture much stronger, 20 rather than five to seven spiral cords, intervarical axial rib stronger, weaker denticles on the outer lip, and an absence of a projecting inner lip.

Pterynotus has only been reported once before from the Paleogene of the Pacific coast of North America. Givens (1974:82) reported three poorly preserved specimens of *Pterynotus* n. sp. from the *Turritella uvasana applinae* fauna ("Domengine Stage") of the Juncal Formation, Pine Mountain area, Ventura County, southern California. The new species differs in the following features: a single intervarical axial rib rather than three and stronger and more closely spaced spiral ribs.

A poorly preserved specimen of *Pterynotus* sp. indet. was found recently by the senior author while examining the LACMIP collection of mollusks from the "Stewart bed" in the Lajas Formation, north side of Simi Valley, Ventura County, southern California. Squires (1984) assigned the "Stewart bed" to the middle Eocene ("Domengine Stage").

Turner (1938) reported the trivariate muricid *Murex* (*Alipurpura*) *coosensis* Turner (1938:80, pl. 15, fig. 25; Weaver, 1942 [1943]:454–455, pl. 88, fig. 19) from the so-called lower and upper Umpqua of southwestern Oregon. Squires (1984) considered the "lower Umpqua" to correspond to the middle lower Eocene ("Capay Stage") Roseburg Formation and the "upper Umpqua" to correspond to the middle lower Eocene ("Capay Stage") Lookingglass Formation and the upper lower to lower middle Eocene ("Domengine Stage") Flournoy Formation. The new species differs from *M. (A.) coosensis* in the following features: three varices on all whorls rather than only on the body whorl and penultimate whorl, winglike varices rather than just thick swellings, and early whorls without seven axial ribs. Although the holotype of *M. (A.) coosensis* is very poorly preserved, examination revealed that it may be a cymatiid.

Another reported trivariate muricid from the Eocene of the Pacific coast of North America is *Murex packardii* Dickerson (1915:69, pl. 9, figs. 6a–6b; Weaver, 1942 [1943]: 455, pl. 88, figs. 17–18) from the upper middle Eocene Cowlitz Formation, southwestern Washington. The new

species differs in the following features: varices more wing-like (especially on outer lip), varices not ruffled, only one rather than two nodose intervarical axial ribs, and spiral ribs weaker and more closely spaced.

The genus *Pterynotus* is one of the most ancient muricine lineages and dates back to at least the Paleocene in Alabama (Vokes, 1964, 1970). During Eocene time, the *Pterynotus* group dominated the muricine world, especially in the warm, shallow seas of the Anglo-Paris Basin (Vokes, 1970). Although *Pterynotus* was widely distributed during the Eocene (Harasewych & Jensen, 1979; Beu & Maxwell, 1990), modern species are restricted to subtropical and tropical regions, usually in moderately deep waters.

The new species is only the second species of *Pterynotus* s.s., including the fossil and Recent record, known from the Pacific coast of North America. No species of *Pterynotus* s.s. occurs in the Panamic province today (Keen, 1971).

Etymology: The new species is named for the state of Washington.

ACKNOWLEDGMENTS

Gail H. Goedert helped collect the fossils. James H. McLean (LACM) gave much help in the identification of the genera. Emily H. Vokes (Tulane University, Louisiana) shared her knowledge of muricines, provided key literature, and reviewed the section on the new species of *Pterynotus*. Alvin A. Almgren (Bakersfield) and R. E. Wells (United States Geological Survey, Menlo Park) shared their knowledge of Eocene stratigraphy of southwestern Washington. Charles R. Givens (Nicholls State University, Louisiana) shared his knowledge of the fossil record of *Pterynotus* on the Pacific coast of North America and provided literature. Mark V. Filewicz (Houston, Texas) processed two microfossil samples and identified the calcareous nannofossils. Ray T. Perreault (Jarreau, Louisiana) identified the barnacles. Jean DeMouthe (California Academy of Sciences, San Francisco) and David R. Lindberg (University of California, Berkeley) arranged for the loan of primary type specimens. Lindsey T. Groves (LACM) provided loans of comparative specimens and access to literature. The manuscript benefited from comments by Ellen J. Moore (Oregon State University, Corvallis) and an anonymous reviewer. Expenses were partially paid by a Conchologists of America grant to the senior author.

LOCALITIES CITED

CSUN 1211. At elevation of 2200 ft. (670 m) on power-line road adjacent to power tower number 395 on E side of mouth of Grapevine Canyon, 2484 m (8150 ft.) N38°W of radio relay station on Grapevine Peak, U.S. Geological Survey, 7.5-minute, Grapevine Quadrangle, 1958 (photorevised 1974), Kern County, California. Liveoak Shale Member of the Tejon Formation. Age: Middle early Eocene ("Capay Stage"). Collector: R. L. Squires, 1988.

CSUN 1567, 1569, 1570. Localities are about 2 m apart, in ascending stratigraphic order, in a 17-m-thick section of sedimentary rocks interbedded with a basalt unit in quarry at E end of bluff overlooking W side of Garrard Creek, latitude 46°45'52"N, longitude 123°19'00"W, 46 m (150 ft.) N and 518 m (1700 ft.) W of SE corner of section 21, T. 15 N, R. 5 W, U.S. Geological Survey, 7.5-minute, Cedarville Quadrangle, 1986, extreme NW corner of Lewis County, Washington. Transition zone of interbedded volcanic and sedimentary rocks between the upper Crescent Formation and the overlying lower member of McIntosh Formation (as used in the emended sense of Pease & Hoover, 1957). Age: Middle Eocene. Collectors: J. L. & G. H. Goedert, 1993–1994.

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NOTES, INFORMATION & NEWS

An Anomalous Specimen of *Petricola stellae* Narchi, 1975, from the Littoral of São Paulo, Brazil

by

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During a survey for bivalves in the littoral of São Paulo, Brazil, the first author had the opportunity to collect a large number of a boring lamellibranch belonging to the Petricolidae. The specimens appeared to be a new species described by Narchi (1975) as *Petricola stellae*. Living specimens and empty shells were obtained from beaches at Porchat Island, São Vicente, and at Santos, respectively. They were found in the intertidal zone, buried in the reefs formed by the polychaete *Phragmatopoma lapidosa* Kinberg, which lie on the mud at the low-water mark.

As observed by Narchi (1975), apparently the species is not able to bore into very hard rocks. Perforations are

made presumably by the opening and closing action of the shell valves, having the hingeline like an axis, as observed by Purchon (1955) in *Petricola pholadiformis* Lamarck, and by Yonge (1958) in *Petricola carditoides* (Conrad). Although the initial settlement of *Petricola stellae* probably takes place in a pre-existing cavity, the hole is enlarged as the animal grows older to form a cavity into which it fits when the valves separate (Narchi, 1975).

Recently, the authors revisited the type locality and found a population of *Petricola stellae* to be present and healthy. Several specimens were collected and transferred to the Malacological Laboratory, Department of Zoology, Biosciences Institute, University of São Paulo.

Observation of this material was made at the Department of Zoology, where live specimens were maintained in Petri dishes and fed on diatoms (*Navicula* sp.). The seawater in the dishes was changed frequently, and the temperature of 21°C was found to be optimal to maintain the animals alive for 3 to 4 weeks.

Among all collected material, some shells exhibited severe distortions owing to the irregularity of the cavities in which they had settled. To our great surprise, among the remaining specimens, one caught the author's attention by

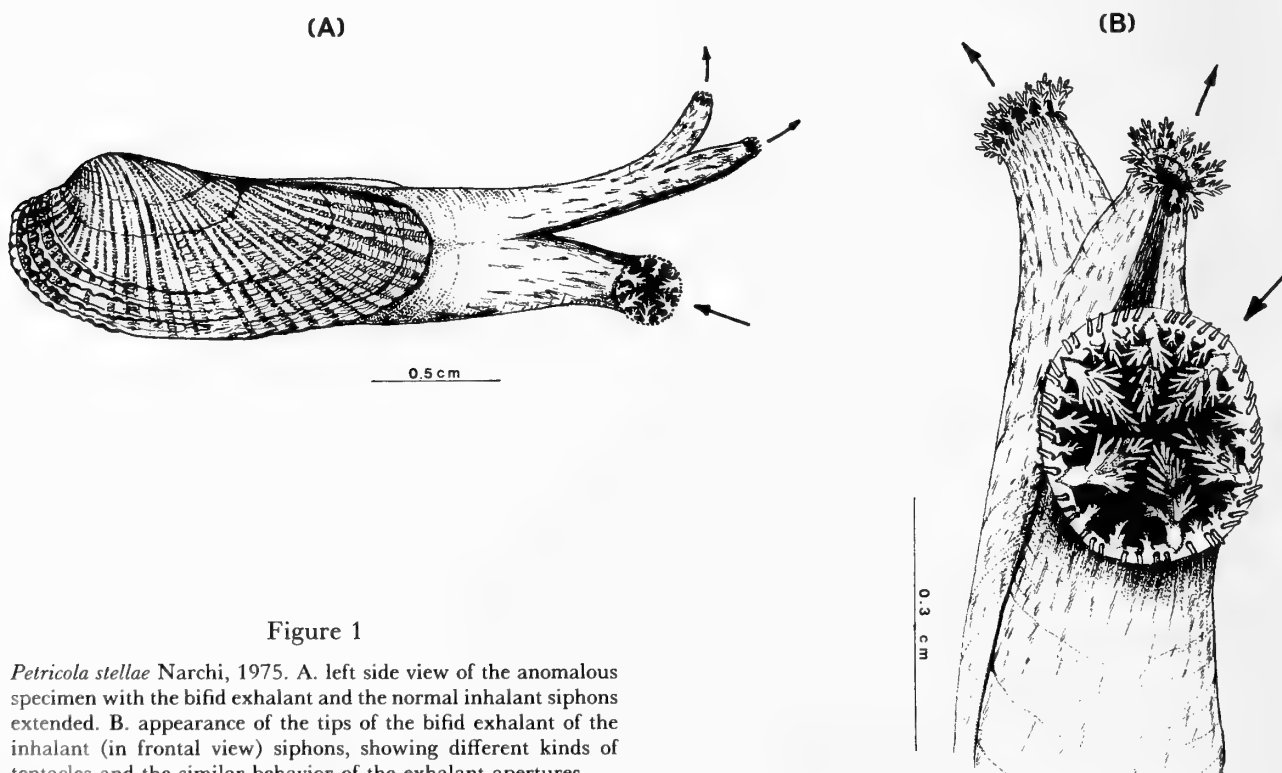


Figure 1

Petricola stellae Narchi, 1975. A. left side view of the anomalous specimen with the bifid exhalant and the normal inhalant siphons extended. B. appearance of the tips of the bifid exhalant of the inhalant (in frontal view) siphons, showing different kinds of tentacles and the similar behavior of the exhalant apertures.

having a bifid exhalant siphon, equipped with two functional apertures (Figure 1).

The siphons of the normal specimens were studied in detail by Narchi (1975) who described them as fused at their basal halves, separate in the distal ones, and exceeding little more than the shell length when fully extended. The same features were found to be present in the anomalous specimen here analyzed. Its siphons are smooth, the flesh being of an opaque cream color with irregular patches of white and light brown pigments. Extending from the separation area between them to their tips, there is a band of brown pigment just as described by Narchi (1975).

The anomalous clam has its inhalant aperture surrounded by a series of regularly branching tentacles of various sizes, classified from primary to quaternary, similar to those of the normal animals; its two exhalant apertures are surrounded by a poorly developed valvular membrane and a variable number of small tentacles which tend to be arranged in three circles, the inner one consisting of pinnate tentacles and the outer circles consisting of two series of simple smaller tentacles, just like the ones described by Narchi (1975) for the species. Nevertheless, the number of pinnate tentacles in the exhalant siphon of the anomalous specimen is half that of a normal one.

The observed abnormality could have resulted from a genetic factor or a mechanical injury sustained early in the juvenile stage, proceeded by regeneration and concomitant formation of a bifid siphon. If the second is the true hypothesis, regeneration of the tissues was accompanied by a normal regeneration of the nervous system since both exhalant apertures exhibited absolutely identical behavior when exposed to flashes of light, shading, mechanical stimulus, or in controlling the flow of water out of them.

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- First Fossil Record for *Myonera*
(Bivalvia: Cuspidariidae)**
by
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- The bivalve genus *Myonera* Dall, 1886, is today widespread in deep-marine environments, but until now this genus had no known fossil record. A single small fossil (Figure 1) recently collected from rocks on the Olympic Peninsula, Washington, is referable to *Myonera*. It is a right valve, resembling that of Recent *M. tillamookensis* Dall, 1916; however, more specimens are needed for species identification. It is preserved on a bedding plane within a concretion containing woody debris, fish scales, and minute pectinids. The concretion was found as "float" eroded from the Makah Formation exposed on the modern beach terrace at Shipwreck Point, Clallam County, Washington (Natural History Museum of Los Angeles County Invertebrate Paleontology locality 8233).
- The Makah Formation was deposited in a deep-water, submarine-fan setting, and is Late Eocene to Late Oligocene in age (Snively et al., 1980; Armentrout et al., 1983). Thin-bedded sandstones and siltstones exposed at LACMIP loc. 8233 represent basin-plain and outer fan-fringe deposition within an ancient deep marginal basin (Snively et al., 1980) and are late early to early late Oligocene in age (Squires et al., 1991; Squires & Goedert, 1994). Megafossils are rare in these strata, but include cetacean skeletons (Squires et al., 1991), deep-water gastropods (Squires & Goedert, 1994), and isopods (Wieder & Feldmann, 1989). Methane-derived authigenic carbonates are also enclosed in siltstone of the Makah Formation at Shipwreck Point (Goedert & Campbell, 1995). Fossils from these carbonates represent a diverse chemosymbiotic invertebrate community that included the bivalve genera *Calyptogena* and *Modiolus* and the gastropod genus *Provanna*, in addition to scaphopods, chitons, and vestimentiferan? worm tubes (Goedert & Campbell, 1995; Squires, 1995; Squires & Goedert, 1995). Prior to the discovery of the chemosymbiotic fauna at Shipwreck Point, the genus *Provanna* also had no fossil record.
- The limestone masses and some of the concretions in the deep-water strata exposed at Shipwreck Point are allochthonous (Goedert & Campbell, 1995); however, *Myonera* would not have been out of place in this deep-marine setting. Records of extant *Myonera* spp. from off the Pacific coast of North America range from 439 m to 3585 m in depth (Coan et al., in press) and are, at least in part, from environments similar to that in which rocks of the Makah Formation accumulated.

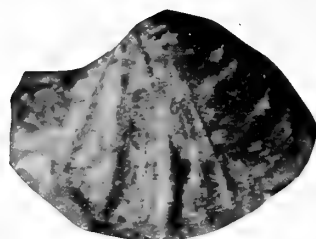


Figure 1

Right valve of *Myonera* sp., $\times 6.8$, Hypotype LACMIP 12367, Makah Formation, Shipwreck Point, Washington, LACMIP loc. 8233. Collected 3 April 1992 by G. H. Goedert.

Acknowledgments

I thank Eugene V. Coan, Ellen J. Moore, and Richard L. Squires for literature and discussions related to this paper, and Edward C. Wilson for locality and specimen numbers. Fieldwork was supported by a National Geographic Society grant (4439-90) to the Natural History Museum of Los Angeles County Foundation, for fossil cetacean research on the Olympic Peninsula, Washington.

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BOOKS, PERIODICALS & PAMPHLETS

Guide to Marine Invertebrates Alaska to Baja California

by DANIEL W. GOTSHALL. 1994. Sea Challengers, 4 Sommerset Rise, Monterey, California 93940. 105 pp. ISBN 0-930118-19-7. \$22.95.

This field guide is intended to help biologists, students, and "weekend naturalists" to identify common subtidal invertebrates that may be encountered during dives from Alaska to central Baja California. Animals observed in the field are to be identified by comparing them with the color photographs that form the basis of the guide. As in previous field guides by Sea Challengers, the color plates are excellent, and the animals have been captured against realistic-looking, natural backgrounds.

After some useful introductory material and a two-page glossary, the guide begins in earnest with a four-page "Pictorial Key to Phyla" (which perhaps should have been called a "Pictorial Key to Animal Groups or Taxa," because the taxa are usually not phylum-level and are identified by their vernacular names). When users encounter an unfamiliar animal in the field, they are encouraged to match the animal with one of the drawings in the pictorial key and then to proceed to the photographs of the indicated group. Most groups can probably be accessed easily using these good quality drawings, but additional drawings of polychaetes, bryozoans, and phoronids would have been useful to cover the range of forms that might be encountered in these groups.

The 253 species covered in the guide include sponges (28 species represented), cnidarians (48), ctenophores (1), flatworms (5), annelids (11), chitons (2), gastropods (24), bivalves (8), cephalopods (5), crustaceans (43), pycnogonids (1), bryozoans (6), brachiopods (1), phoronids (1), echinoderms (51), and urochordates (18).

Each of the 253 species is identified by a color photograph, a vernacular name, and a scientific name. The text accompanying each photograph provides information on identification, size (English and metric units), range, and habitat; a note on natural history is included for some species. Three species are covered on each page, and the amount of text is limited by the space available next to the photograph.

The book ends with indexes to the common and scientific names of the covered species.

What the book sets out to do it accomplishes fairly well: the guide will allow users to identify easily and accurately many invertebrates observed while diving. The photographs are excellent, and an impressive list of specialists have helped with species identifications or served as editorial consultants.

The few "deficiencies" of the book are largely intended, intrinsic to the approach taken, or readily acknowledged

by the author. They are worth noting, however, as they may influence a decision to buy or not. First, natural history information is scarce and seems almost haphazardly appended to some entries and missing from others. Although the book is intended as a field identification guide, my preference would have been for more information throughout: explain, for example, that nematocysts are of more than one type, why *Stomphia coccinea* has the vernacular name the "swimming anemone" (page 29), that *Pycnopodia* is not only eaten by king crabs but does a lot of eating itself, and so on. Second, land-bound explorers may be disappointed not to find common intertidal species such as *Tegula funebris*, various limpets, mussels, shore crabs, and the like in a book titled "Guide to Marine Invertebrates"; these animals are not included, either because of the subtidal focus of the book or because animals less than 12 mm in length are generally excluded. Third, some groups are given more complete coverage than others: enthusiasts of crustaceans (43 species represented) and echinoderms (51) will be more pleased than those interested in gastropods (24) or bivalves (8). The gastropods, for example, were purposefully slighted, owing to the pre-existence of several good guides on this group. Among the gastropods covered, abalone abound (7 species) but nudibranchs are not to be found.

Other quibbles include some uneven typesetting that does not always match the consistently excellent quality of the color printing and a small assortment of typographical or editorial errors, hopefully to be corrected in later printings ("pliopod" on page 59, "mulluscs" on page 82, and the statement that "sperm is produced only by large older females" on page 27). Indeed the book nearly ends with a humorous typo, which identifies a common tunicate as "Eunerdmania" (page 100, repeated in the index) named, it seems from the new word roots, after a truly crazy computer whiz instead of Dr. Herdman.

These small deficiencies, however, do not detract much from the successful production of an identification guide to the common subtidal invertebrates of our Pacific coast. They simply represent my preference for more information, which the author has chosen not to provide in this particular book. Indeed, Gotschall advises that this field guide should be used in conjunction with other books, such as *Between Pacific Tides* or *Intertidal Invertebrates of California*, and I echo that advice. The question really becomes, should someone who already owns those two also buy Gotschall's *Guide to Marine Invertebrates*? I suggest yes. The book is an accurate, easy-to-use, compact field guide, perfectly suitable for a preliminary identification of commonly encountered subtidal invertebrates. As a bonus, the magnificent color photographs will look great on the coffee table when one is finished with a day in the field.

D. Phillips

**Types of Shelled Indo-Pacific
Mollusks Described by
William Harper Pease (1824–71)**

by RICHARD I. JOHNSON. 1994. *Bulletin of the Museum of Comparative Zoology* 154(1):1–61.

William Harper Pease described some 500 species of mollusks from the Indo-Pacific region. Most of the approximately 380 shell-bearing species, marine and non-marine, are represented by type material in the Museum of Comparative Zoology, Bernice P. Bishop Museum, Academy of Natural Sciences of Philadelphia, and other museums. This bulletin catalogues those species and their type material. (The Baja Californian *Murex foveolatus* Pease, 1869, has found its way in here as well). Many type specimens are illustrated, on nine plates of photographs.

Numerous lectotypes are designated—a necessity under the Code in cases where holotypes were not specified in the original publications. The designations usually appear to be based on specimens previously labeled as holotypes, but in some cases the rationale for the choice of a given specimen is not stated. Lectotype designations by previous authors are noted.

This catalogue brings together information from many disparate sources and will be an aid to workers for years to come.

B. Roth

Galapagan Mollusks

The Marine Mollusks of the Galapagos Islands: A Documented Faunal List by Yves Finet. 1994. Editions du Muséum d'Histoire Naturelle de Genève. Soft cover, 180 pp. ISBN 2-88139-001-3. \$40.00 from US distributors.

Marine Molluscs of the Galapagos, Gastropods, A Monograph and Revision of the Families Haliotidae, Scissurellidae, Fissurellidae and Lottiidae by Yves Finet. 1994. Monographs on Galapagos Mollusca, no. 1. L'Informatore Picena, Ancona, Italy. Glossy hard cover, 110 pp., 26 pls. ISBN 88-86070-08-X. \$40.00 from US distributors.

These two volumes (21 × 30 cm) represent the latest, and most detailed, in a continuing series of publications on mollusks of the Galapagos Islands by Yves Finet of the Muséum d'Histoire naturelle de Genève, Switzerland. Finet's work on Galapagos mollusks is based on visits to US museums in 1983 for study and photography of museum holdings and his trips to the Galapagos Islands in 1984 and 1993. In earlier checklists (Finet, 1985, 1991), museum sources for the records were not indicated. His 1991 effort included a detailed analysis of biogeography.

The "documented faunal list" is unillustrated, except for the cover photograph and unidentified drawings of shells throughout the text. Species are assigned consecutive numbers; a total of 718 are listed. Each entry includes the mention of synonyms (if any), authors and dates for references (but no pagination), and museum catalog numbers for examined specimens (but no locality details). Additionally, in Part II there are 228 taxa that are considered to be rejected records of other authors. Each of these is annotated. One page is devoted to discussion on the taxonomic composition of the fauna, and there is a table in which shallow-water and deep-water species are counted by class and assigned to endemic or non-endemic categories. Overall, 20% of the species are considered endemic; of the shallow-water species, only 16% are considered endemic. Progress has been made in more accurately characterizing the Galapagan molluscan fauna, considering that 40% of the Galapagan fauna from Keen's (1971) *Sea Shells of Tropical West America* was then considered endemic.

The hard-cover volume on the Haliotidae, Scissurellidae, Fissurellidae, and Lottiidae treats 18 species occurring at the Galapagos Islands and discusses 14 species for which a Galapagos occurrence is doubted. Type specimens and other specimens of each species are illustrated in 25 color plates of shells, up to 16 views per plate. In most cases, each species fills a full plate. There are also six half-page, color views of shorelines in the Galapagos. An additional plate has four SEM views of the radula of *Fissurella obscura* Sowerby, 1835.

Each species is treated with full synonymy, and headings for type material and type localities (including paratypes), copies of original descriptions of nominate taxa and synonyms, an additional diagnosis for taxa in which original descriptions are in Latin, a summary of distribution, and a detailed list of material examined, including catalog number and locality details other than coordinates. The locality data for each species is exhaustive and may take more than a full page. Only some of the treated species include a remarks section.

The treatment of the rejected species is detailed, and the illustrations of species not from the Galapagos fill seven plates. The unwary reader may fail to note that the captions for illustrations of type material of synonyms use the original combination and do not refer to the name under which the synonym is placed in the text.

There are few departures from the arrangement of species in these families by McLean in Keen (1971), except that two subsequently described species of *Lottia* are included, and a lectotype is designed for *Fissurella macrotrema* Sowerby, 1835, which rightly serves to place the name in the synonymy of *F. virescens* Sowerby, 1835. The specimen figured as *F. macrotrema* by McLean in Keen (1971) is now redetermined as *F. obscura*.

This reviewer wonders whether the lavish format adopted for the first volume in the series can be sustained, considering that only 18 of the 718 species recognized at

the Galapagos have now been treated, and at rather a high price per species. Finet's color photography is superb, but perhaps a more rewarding effort would be to illustrate all species from the Galapagos under one cover. Now that the museum catalog numbers of the specimens examined by Finet are recorded in the "documented faunal list," there would be little need to include such extensive detail for the localities.

James H. McLean

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- KEEN, A. M. 1971. Sea Shells of Tropical West America. Stanford University Press: Stanford, California. xiv + 1064 pp.

North Pacific Bivalves

Two substantial papers have recently been produced in Russia on the bivalves of the North Pacific. One is a checklist, the other a lengthy biogeographic analysis. Limited copies are available from the author, Alexander I. Kafanov, Institute of Marine Biology, Vladivostok 690041, Russia, in exchange for other literature on Recent and Cenozoic bivalve and marine biogeography.

Dvustvorchatye molliuski i faunisticheskaia biogeografia Severnoi Patsifiki [Bivalve mollusks and faunistic biogeography of the Northern Pacific.] by ALEXANDER I. KAFANOV. "1991" [13 July 1994]. Akademiia Nauk SSSR, Dal'nevostochnoe Otdelenie, Institut Biologii Moria. 195 pp.

According to the English abstract to this volume, "Bivalve molluscs of the shelf and continental slope are used as an example in the study aimed at development of approaches, principles and methods of faunistic biogeography. It is shown that analysis of species richness is the main operational method in faunistic biogeography. The effect of environmental temperature is studied in detail as a factor of species richness while size of biogeographical units and the range of taxa are considered with respect to biogeographical division. An integrated approach to division of intertidal, subtidal and bathial [*sic*] biotas was substantiated. An original scheme is given for faunistic division of the northern Pacific. The monograph is of interest to biogeographers, specialists in ecology and systematics, for teachers and students of biology."

Clearly, this work would be a prime candidate for translation into English. It should be noted that this work was

sent to press in 1989, before the paper by F. R. Bernard, S. M. McKinnell & G. S. Jamieson, "Distribution and zoogeography of the Bivalvia of the eastern Pacific Ocean," Canadian Special Publication of Fisheries and Aquatic Sciences 112: 60 pp., 1991, had appeared.

Dvustvorchatye molliuski shel'fov i kontinental'nogo sklona Severnoi Patsifiki [Bivalve mollusks of the shelf and continental slope of the Northern Pacific] by ALEXANDER I. KAFANOV. Akademiia Nauk SSSR, Dal'nevostochnoe Otdelenie, Institut Biologii Moria. 198 pp. 1992.

This is a checklist, listing synonyms, of the bivalves of the North Pacific. Coverage seems to extend to southern Japan and southern California.

Gene Coan

Australian Marine Shells. Prosobranch Gastropods Part One. 1993. Part Two (Neogastropods). 1994

by BARRY WILSON. Odyssey Publishing, Kallaroo. Volume 1, 408 pp., figs; Volume 2, 370 pp., figs. Price from US distributors, \$85 each volume.

The marine malacofauna of Australia is both diverse and abundant, a reflection of the island continent's exposure to both tropical and temperate environments with their many habitats. As a result, there are an estimated 10,000 species found in the coastal waters, which is probably an understatement given the poorly known microfaunas. With this great abundance of species, there have only been limited attempts at comprehensive reviews, as with Allan's general work in 1950 (later revised to 1959), and the present author's compendium in 1971 (with K. Gillett) which illustrated about 600 species. Other authors have restricted themselves to regional studies, such as the series on southern Australia by Cotton (1940–1963) or Macpherson and Gabriel on Victoria (1962). Clearly no one work can be expected to be exhaustive, but a major contribution toward further appreciating the marine snails of Australia has been made by these two volumes, which discuss and figure over 2400 species.

The author has restricted the scope of his survey to the marine "prosobranchs," which is to say nowadays that he does not discuss the heterobranchs or opisthobranchs. Acknowledging the great changes occurring in the systematics of the higher groups of gastropods, the author has followed the classification system outlined by Ponder and Warén (1988) in arranging the groups for the discussion of species. Many of the lesser gastropod families are mentioned, albeit superficially, and are among the 600 taxa figured within the text using the concise drawing of Carina Wilson. This is a significant accomplishment in its own right given the dearth of information on many of these groups. However,

the emphasis is clearly on the families of marine snails which have the greatest popular appeal and are the best known.

Volume One covers groups from the limpets to the eulimids, with a detailed study of the endemic cowries as well as introductory sections on collecting, conservation, and classification. The second volume covers the neogastropods with comprehensive sections on the muricids, volutes, and cones. The hallmark of each volume is the superb color illustrations, arranged in a total of 97 plates, which are among the best ever published. Each species is given a concise written description with comments regarding range of distribution and synonymy. Genera are described and accompanied with a listing of the type species. There is only one map in each volume, which may be a nice visual, but lacks many localities mentioned in the text.

The text in both volumes is remarkably free of errors, and each index lists taxa with authors and dates. I would have preferred to have had a unified bibliography instead of having full citations listed throughout the text, and to have had author and date listed with each species in the plate captions, but these are minor quibbles. More im-

portantly, the author should have given the source of each illustrated figure in an appendix, a very useful practice that was followed by Myra Keen. This lack of information is particularly aggravating when a type specimen has been illustrated without any indication as to where it is housed.

In general, however, these works represent a major positive contribution toward the appreciation of the Australian mollusks and will quickly become an indispensable part of the malacological library. Each volume has broad appeal to all those working on Indo-Pacific marine snails, and given the spectacular cover design and color, it is not likely one will misplace either of them in the clutter of one's office or workroom.

Henry Chaney

Literature Cited

- PONDER, W. F. & A. WARÉN. 1988. Classification of the Caenogastropoda and Heterostropha—a list of the family-group names and higher taxa. *Malacological Review*, Supplement 4:288–326.

Manuscripts

Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

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Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles *unabbreviated*, and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245-272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117-135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

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Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend. Avoid vertical rules.

Figures and plates

Figures must be carefully prepared and submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited. Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures. Photo-

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Clear xerographic copies of figures are suitable for reviewers' copies of submitted manuscripts. It is the author's responsibility to ensure that lettering will be legible after any necessary reduction and that lettering size is appropriate to the figure.

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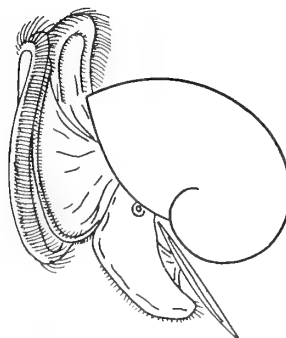
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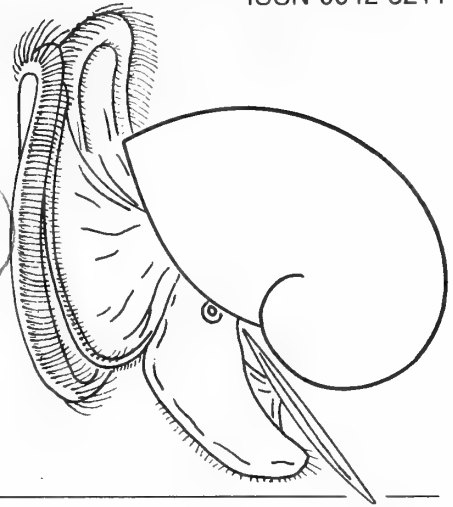


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CALIFORNIA MALACOOZOLOGICAL SOCIETY, INC.
Berkeley, California
R. Stohler, Founding Editor

Volume 38

October 2, 1995

Number 4

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The *Veliger* (ISSN 0042-3211) is published quarterly in January, April, July, and October by the California Malacozoological Society, Inc., % Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105. Second Class postage paid at Berkeley, CA and additional mailing offices. POSTMASTER: Send address changes to *The Veliger*, Santa Barbara Museum of Natural History, 2559 Puesta del Sol Road, Santa Barbara, CA 93105.

THE VELIGER

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Food and Feeding in *Pomacea canaliculata* (Gastropoda: Ampullariidae)

by

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Abstract. Food preferences, growth rates on different aquatic plant diets, and the ability to detect distant food sources were studied in the ampullariid snail *Pomacea canaliculata*. The snails actively select their food. No ontogenetic differences were detected in feeding preferences. The most preferred macrophyte was *Zannichellia palustris*, followed by *Myriophyllum elatinoides*, and *Chara contraria*. The snails showed a low preference for *Rorippa nasturtium-aquaticum* and *Potamogeton striatus*, whereas *Elodea canadensis* was not selected. The growth experiments reflected this behavior; snails reared on *Zannichellia* reached the largest sizes, followed by those fed on *Myriophyllum*. No statistical differences were detected in the size of snails reared on *Rorippa* and *Potamogeton*. The results obtained in distant chemoreception experiments support the hypothesis that *P. canaliculata* is able to detect chemical signals from some distance. This ability remains unaffected whether the stimulus source was positioned on the left- or on the right-hand side of the Y-chamber.

INTRODUCTION

Unlike the majority of the freshwater snails which are microphagous, apple-snails belonging to the Ampullariidae family show three feeding types (not mutually exclusive): microphagous, zoophagous, and macrophytophagous. The microphagous habit includes radular grazing on the *Aufwuchs* (Ferguson, 1978), deposit feeding (Nono & Mane, 1931), and surface film feeding (Johnson, 1952; McClary, 1964). Some apple-snails feed on insects, crustaceans, small fish, etc. (Villela, 1956; Van Coille et al., 1978), but the most studied zoophagous habit of these snails is predation on eggs, spat, and adults of bilharzia snail hosts (Demian & Lufty, 1965a, b). The macrophagous type is the most common in *Pomacea canaliculata* (Lamarck, 1801); it feeds preferentially on macrophytic vegetation (Cazzaniga & Estebenet, 1984).

Aquatic plants have traditionally been considered as important to freshwater snail populations, mainly in their capacity as a physical support for egg masses, as refuge against predators, and as a substrate for the periphyton the snails feed upon. Some authors, however, have stressed the importance of herbivory (or consumption of macrophytes) in freshwater systems, noting that more data on trophic preferences and feeding habits in herbivorous invertebrates are necessary (Lodge et al., 1987; Lodge, 1991; Newman, 1991).

The aims of this study were: (1) to determine if young and adult *P. canaliculata* snails have the same preferences for different macrophytes that occur naturally with the snails; (2) to evaluate the effects of different aquatic plant diets on the growth of the snails; and (3) to determine if distant chemoreception is involved in food selection.

MATERIALS AND METHODS

Feeding Preference Experiments

Young and adult snails were collected from an artificial pond in La Plata city (Buenos Aires province, Argentina) and maintained in aerated tap water ($25 \pm 1^\circ\text{C}$) until experiments began. The shell height ranges of two age classes of snails were as follows: young, 10–25 mm high and adult, 35–48 mm high.

Zannichellia palustris L., *Potamogeton striatus* Ruiz & Pavon, and *Rorippa nasturtium-aquaticum* (L.) Hayek were collected from the Napostá Grande stream within the city of Bahía Blanca. *Chara contraria* A. Braun ex Kütz. and *Myriophyllum elatinoides* L. were collected from a canal filled with Napostá Grande stream water. *Elodea canadensis* Michx. was collected from a pool located in the campus of the Universidad Nacional del Sur. The macrophytes were brushed to remove periphyton, refrigerated, and used within 3 days of collection.

In order to determine snail food preferences, 70-liter aquaria were divided into eight equal food compartments with one longer central compartment for introducing the snails into the system. In each trial, three macrophytes were randomly distributed among the compartments. Two compartments received *Zannichellia*, two received *Myriophyllum*, two received *Chara*, and the remaining two compartments were used as controls (with no food) (Experiment 1). Twenty snails were introduced into the center of the aquarium, and the number of snails in each compartment was recorded 4 hr later. Since the number of animals leaving the introduction compartment was not the same in each trial, the proportion of the number of snails in each food compartment to the total number of moving snails was used for the analysis. The trials were performed with young and adult snails separately. The experiment was repeated 32 times. However, these repetitions are not true replicates (in a statistical sense) because after determining the number of snails in seven of the eight possible locations, the number of snails in the last compartment is necessarily fixed. So 32 repetitions were necessary to obtain eight independent observations in each food compartment. These replicates were randomly selected from the 32 repetitions.

The feeding preferences were tested with an analysis of variance with a factorial (two ages \times four food types) arrangement of treatments and with Scheffé's multiple comparison test (Sokal & Rohlf, 1979). Similar experiments (Experiments 2 to 6) were performed with other combinations of aquatic plants, each new experiment being designed according to the results of the previous one. The objective of this sequential design was to avoid testing superfluous combinations.

Food and Growth

Zannichellia palustris, *E. canadensis*, *R. nasturtium-aquaticum*, *M. elatinoides*, and *P. striatus* were used as diets in the growth experiments. Only small snails were used, no ontogenetic differences in the food preferences having been detected previously (see Results).

Seventy-five snails from a single egg mass were used. From these, 15 snails, 2.4–2.9 mm high, were randomly selected for each diet. The snails were placed in 3-liter aquaria with tap water (hardness 90–96 ppm CaCO_3). The snails were reared at room temperature with a natural photoperiod. The food was provided *ad libitum* in all cases.

Each week the height of the shell (from the shell apex to the aperture basal extreme) was measured under a stereoscopic microscope to the nearest 0.01 mm, or with a caliper to the nearest 0.1 mm (depending on the snail size). The experiments were conducted during 115 days (summer 1987/1988). The final size differences among snails reared on the various diets were analyzed by one-way ANOVA and by Scheffé's multiple comparison procedure (Sokal & Rohlf, 1979).

Distant Chemoreception

Approximately 200 adult snails, 33.00 to 45.4 mm high, were used. The reaction of the snails to different aquatic plants was determined by observing their behavior in a Y-maze made of glass strips. The stem of the Y-maze was 20 cm long \times 8 cm wide, the two arms diverging 45° from one another and measuring 10×8 cm. The Y-maze was filled with warm tap water ($25 \pm 1^\circ\text{C}$) up to a level of 6 cm.

Zannichellia palustris, *M. elatinoides*, *R. nasturtium-aquaticum*, and *E. canadensis* were used as stimuli sources. The food was alternately located at the distal end of one arm of the Y-maze, and a snail was placed at the base of the stem. The position of the snail was recorded at 15 minute intervals, and the trial was concluded either when it had moved 5 cm along one arm or after one hour. A similar trial was conducted with no food to determine the pattern of motion of the snails. All snails were deprived of food for 3 hr before the trial. Each experiment was replicated 56 times, and the data were analyzed by the chi-square test.

RESULTS

Feeding Preference Experiments

Figure 1 shows the results of the six food preference experiments. In all of them, the age \times food type interaction was not significant (Table 1), indicating that the two factors are independent. Since no ontogenetic food preferences were detected (Table 1), the results of young snails were pooled with those of adults. Not all possible combinations of aquatic plants were tested, and the rank order of food preference was determined by transitivity of experiment results.

Zannichellia palustris was alternatively combined with *M. elatinoides*, *Ch. contraria*, *P. striatus*, and *R. nasturtium-aquaticum* (Experiments 1 to 3 and 5). It was the most preferred diet in the four experiments (Figure 1). The snails also showed a high preference for *M. elatinoides* followed by *Ch. contraria*; *Potamogeton striatus* and *R. nasturtium-aquaticum* were the least preferred macrophytes; the number of snails in the compartment with *Elodea* did not differ from that in the control compartment.

The snails showed a high level of activity in all the trials, irrespective of the offered combination of aquatic plants. The percentage of mobile snails ranged from 57% to 89.2% in the case of young snails and from 61.9% to 84.2% in the case of adults.

Food and Growth

Figure 2 shows the growth of the snails reared on five different macrophytes. One week after commencement of the experiment, significant differences were detected in the growth of the snails reared on different macrophytes. The snails fed on *Elodea* were smaller than the other groups; they only grew during the first 10 days, after which period

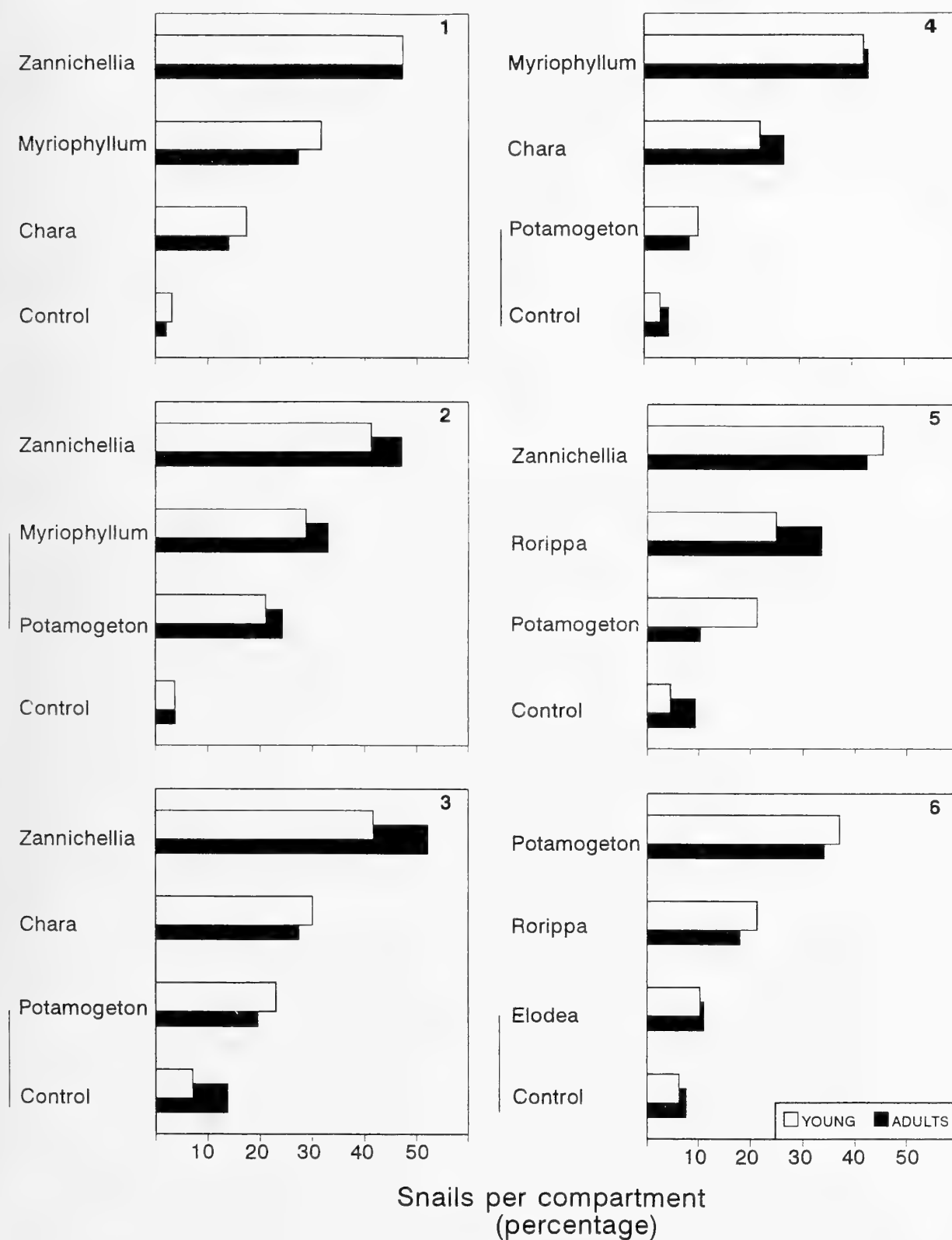


Figure 1

Results of the feeding preference experiments. There are no significant differences in feeding preferences between the aquatic plants (and/or control) linked by vertical bars (Scheffé's multiple comparison procedure, $P > 0.05$).

Table 1

Analyses of variance for differences in feeding preferences.

Experiment Source of variation	SS	d.f.	F
Experiment 1			
Between treatments	1.77	7	27.24**
Age	0.011	1	1.18
Food	1.757	3	63.11**
Age × food	0.002	3	<1
Error	0.52	56	
Experiment 2			
Between treatments	1.395	7	9.92**
Age	0.017	1	<1
Food	1.3708	3	22.78**
Age × food	0.0066	3	<1
Error	1.125	56	
Experiment 3			
Between treatments	1.1997	7	7.30**
Age	0.0121	1	<1
Food	1.1304	3	16.06**
Age × food	0.0571	3	<1
Error	1.3143	56	
Experiment 4			
Between treatments	1.454	7	17.32**
Age	0.0033	1	<1
Food	1.442	3	40.08**
Age × food	0.0086	3	<1
Error	0.6716	56	
Experiment 5			
Between treatments	1.3294	7	11.90**
Age	0.0002	1	<1
Food	1.2378	3	25.86**
Age × food	0.0914	3	1.91
Error	0.8934	56	
Experiment 6			
Between treatments	0.7866	7	27.80**
Age	0.0017	1	<1
Food	0.7777	3	64.15**
Age × food	0.0071	3	<1
Error	0.2263	56	

** $P < 0.01$; all others not significant.

Table 2

Analysis of variance table and Scheffé's multiple comparison test for the growth of snails reared on four different macrophytes.

Source of variation	SS	d.f.	F
Between macrophytes	1452.64	3	37.17**
1) <i>Zannichellia</i> - <i>Myriophyllum</i> vs. <i>Rorippa</i> - <i>Potamogeton</i>	1254.46	1	$f_1 = 134.63^{**}$
2) <i>Zannichellia</i> vs. <i>Myriophyl-</i> <i>lum</i>	184.52	1	$f_2 = 19.80^{**}$
3) <i>Rorippa</i> vs. <i>Potamogeton</i>	13.66	1	$f_3 = 1.47^{NS}$
Error	521.83	56	
Total	1974.47	59	

** $P < 0.01$; NS: $P > 0.05$.

some died and the others were inactive. This group was therefore disregarded in subsequent observations.

Highly significant differences existed among the mean final sizes attained by the snail sets, attributed to the different aquatic plants consumed. The snails reared on *Z. palustris* grew more than those reared on other macrophytes, followed by those fed on *M. elatinoides*. No significant growth differences between the snails reared on the remaining two macrophytes were found (Table 2).

Distant Chemoreception

Table 3 shows the results of the experiments using the Y-maze. With no food, the movement of the snails to the left or the right arm in the Y-maze was random.

The number of snails entering into the arm with *Z. palustris* was greater than the number of snails entering into the empty arm, suggesting that this macrophyte is highly attractive to *P. canaliculata*.

The movement of the snails when *M. elatinoides* or *R. nasturtium-aquaticum* were used as a source of stimuli was random. A completely different motion pattern was observed when *E. canadensis* was used as the source of stimulus. In approximately 55% of the replicates, the snails remained at the base of the stem, some of them retracting into their shell and remaining in that position until the

Table 3

Number of snails entering into one of two arms in the Y-maze. Each experiment was replicated 56 times. The food source was located 28 times in each arm of the Y-maze (F: food; E: empty).

	<i>Zannichellia</i>		<i>Myriophyllum</i>		<i>Rorippa</i>		<i>Elodea</i>		No food
	F	E	F	E	F	E	F	E	
Left arm	19	8	13	8	16	10	1	3	19
Right arm	17	4	15	12	9	7	8	14	28
Total	36	12	28	20	25	17	9	17	47
Snails mobilized (%)	85.71		85.71		75.00		46.42		83.92
χ^2	12**		1.33 ^{NS}		1.52 ^{NS}		—		1.72 ^{NS}

** $P < 0.01$; NS: $P > 0.05$.

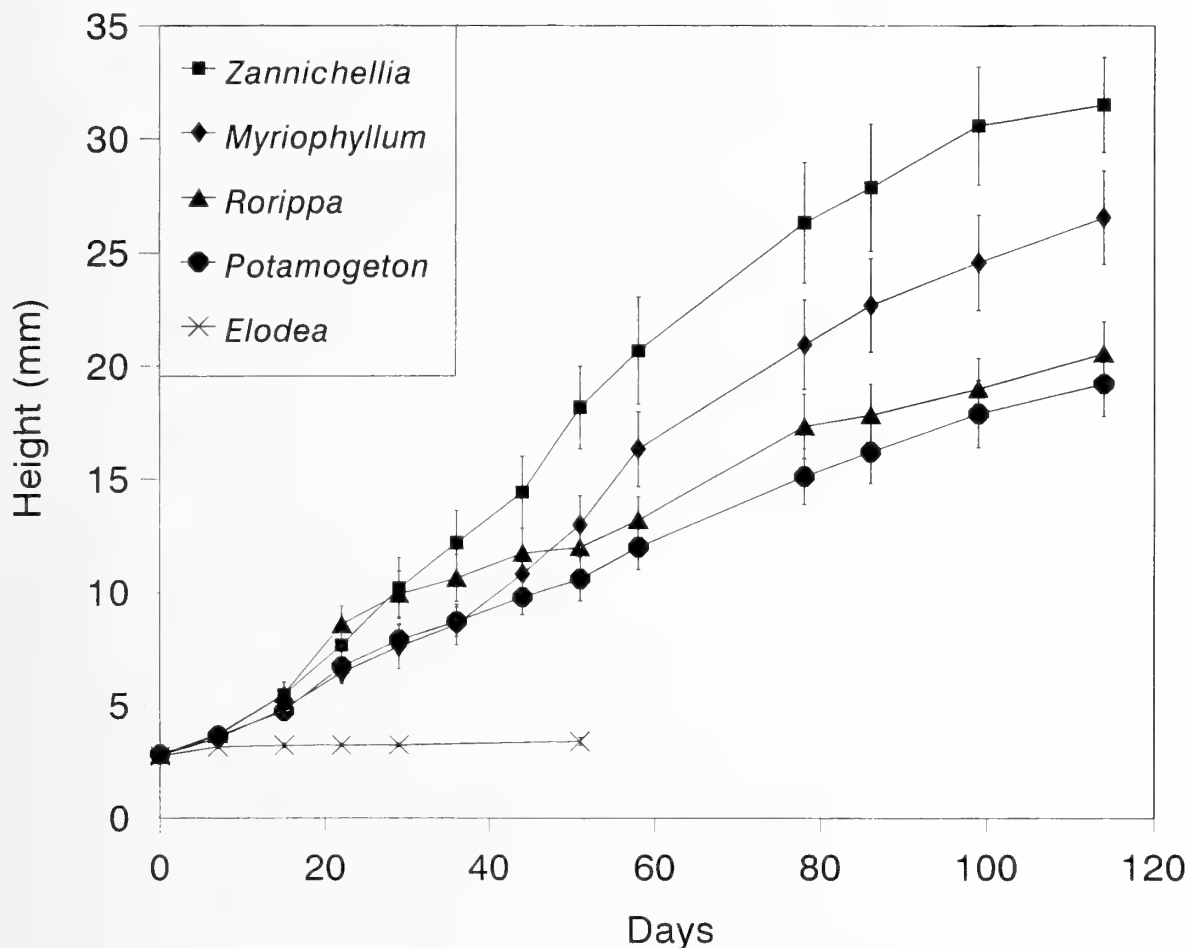


Figure 2

Growth of snails reared on five different macrophytes (mean \pm 95% confidence interval).

trials concluded. Only 34.62% of the mobile snails entered the arm containing *Elodea*; the remaining 65.38% went to the empty arm. No statistical test was performed, since the number of snails moving on was very different from the results of the other experiments, bearing no comparison.

DISCUSSION

Although *Pomacea canaliculata* is a generalized herbivore, it nevertheless actively selects its food. The same behavior has been described in other freshwater snails: *Marisa cornuarietis* (Linnaeus) (Rich & Rouse, 1970; Cedeño-Leon & Thomas, 1982), *Biomphalaria glabrata* (Say) (Cedeño-Leon & Thomas, 1982), *Lymnaea elodes* Say and *Aplexa hypnorum* (Linnaeus) (Brown, 1982), and *Physa gyrina* (Say) (Sheldon, 1987). *Zannichellia palustris* was the macrophyte most preferred by the apple-snails, followed by *M. elatinoidea* and *Ch. contraria*. *P. canaliculata* shows moderate to low preference for *R. nasturtium-aquaticum* and *P. striatus*. The only aquatic plant to be totally rejected was *E. canadensis*.

On the basis of the percentage of plant species eaten by snails during a 24 hr period, Cedeño-Leon & Thomas (1982) stated that juvenile *Marisa* has broader niches than adult snails. In the present paper, the number of snails on each macrophyte was considered as an index of food preference, and no ontogenetic differences were detected. The results regarding the level of activity showed by young and adult snails are not conclusive, and on the basis of the recorded variation, the hypothesis of similar activity cannot be rejected. Louda & McKaye (1982) also showed the movements of different sized snails to be similar in the ampullariid *Lanistes nyassanus* Dohrn.

The low degree of herbivory on freshwater macrophytes has been attributed to one or more of the following factors: the poor quality of vegetal material as food, structural plant defenses, and secondary plant substances (Thomas, 1987). The majority of pulmonate freshwater snails do not include live aquatic plants in their diet (Hunter, 1980; Reavell, 1980; Brönmark, 1990), and the tough outer envelope of macrophytes has been mentioned as one of the main barriers. Ndifon (1980, cited in Cedeño-Leon & Thomas,

1982) showed that *Bulinus globosus* (Morelet) loses radular teeth when feeding on macrophytes because its radula (and those of the freshwater pulmonates in general) is apparently not adapted to this habit (Thomas, 1982). At least two other freshwater pulmonate snails lose numerous teeth during feeding, although macrophytes do not form a part of their diet. This is the case with *Physa venustula* Gould and *Chilina parchappii* (d'Orbigny), both of which eat almost exclusively *Aufwuchs* and detritus (personal observation). These snails scrape the algae, bacteria, and invertebrates attached to submerged hard surfaces. The feeding is an almost uninterrupted activity so the radula is under severe strain and wear, being replaced continually (Mackenstedt & Markel, 1987). Almost all teeth found in stomachs and feces show very eroded cusps. The gut of *Pomacea canaliculata*, however, is specially adapted to macrophagous habits (Andrews, 1965) so that structural plant defenses are not effective.

The poor quality of aquatic plants does not seem important since Lodge (1991) and Newman (1991) have demonstrated that the N content is similar in aquatic and terrestrial plants. Moreover, some aquatic herbivorous invertebrates prefer macrophytes of lower nutritional value if they are easier to handle (Chambers et al., 1991).

Lindstedt (1971) stressed that the absence of feeding inhibitors (repellents, suppressants, or deterrents) is just as important as the presence of feeding activators, or even more so, in determining the acceptability of a food item.

Thomas (1982) and Cedeño-Leon & Thomas (1982) stated that aquatic plants (including some of the macrophytes used in the experiments presented in this paper) do not have any chemical or molluscicide properties. More recently, however, Ostrofsky & Zettler (1986) determined 15 species of aquatic plants with compounds that are toxic to invertebrates. In the list of material analyzed, some species of *Potamogeton* and *Myriophyllum*, and *Elodea canadensis* are mentioned. Although the range of alkaloid concentrations is low, these authors suggested that their results are consistent with a potential role as herbivorous deterrents. Lodge (1991) has suggested that phenolics are more important than alkaloids in determining food choice by herbivores in freshwater. In the food preference experiments, *E. canadensis* was offered as a choice together with two low-preference macrophytes. However, the number of snails in the compartment with *Elodea* did not differ from that in the control compartment. In the growth experiments, the snails reared on this aquatic plant grew only 0.5 mm in a month. This low increase was not due to the ingestion of food but rather to the consumption of vitelline material stored in the liver. In the Y-chamber experiments, *P. canaliculata* rejected *Elodea*. Although there is no statistical corroboration of this assertion, it is based on the differential behavior of the snails when *Elodea* is presented as a stimulus source. These experiments thus suggest that *P. canaliculata* is able to detect from some distance certain chemical compounds released by *E. canadensis* that act as repellents to snails. Other invertebrate species (including

freshwater snails) also reject *Elodea* as a food source when it is present either alone or in combination with other macrophytes. These results are not in agreement with those obtained by other authors using *Elodea* as a source of food for the ampullariid snail *Marisa cornuarietis*. While Seaman & Portfield (1964) stated that *Elodea* is only ingested as a last resort, Cedeño-Leon & Thomas (1982) showed it to be the most preferred aquatic plant (from 10 offered) by both young and adult *M. cornuarietis* snails.

In the food preference experiments, *Z. palustris* was the aquatic plant most preferred by snails, followed by *M. elatinoides*. These results agree with those of the growth experiments where snails reared on *Z. palustris* showed the largest sizes, followed by those reared on *M. elatinoides*. The difference in the final sizes attained by the two groups was caused by the higher rate of *Z. palustris* ingested (2.31 g fresh weight/snail/day, on day 25) compared with *M. elatinoides* (1.02 g fresh weight/snail/day).

Although Michelson (1960) and Bousfield (1979) suggested *Rorippa* releases chemical substances that repel *B. glabrata*, *P. canaliculata* never rejected this aquatic plant. Calow & Calow (1975) stated that starved snails become less selective. However, the ingestion rate on this macrophyte was less than that observed on most preferred aquatic plants. Olazarri (1979) refers to *P. canaliculata* as a watercress pest, but this assertion was based on the snail egg masses deposited on the plant, which cause a deterioration in the product from the commercial viewpoint, and could be toxic (Snyder & Snyder, 1971).

The results obtained using the Y-chamber support the hypothesis that *P. canaliculata* is able to detect chemical signals (attractants and repellents) from some distance. The position of the stimulus source on the left- or the right-hand side of the Y-chamber has no effect on such detection ($\chi^2 = 1.37$, $P > 0.20$). Other freshwater snails use distant chemoreception to locate food sources (Michelson, 1960; Bovbjerg, 1968; Lombardo et al., 1991), and McClary (1964) asserted that the ampullariid *Pomacea paludosa* can detect food on a surface film from a distance of several centimeters. Tentacles, osphradium, and labial palps have been pointed out as receptor organs (Croll, 1983). The osphradium is the probable distance chemoreceptor as shown by studies on its development, anatomical constitution, innervation, and location in various snail species. Keawjan (1987) attributed a similar function to the osphradium of *Pila*.

The presence of efficient chemoreception mechanisms could give *P. canaliculata* an adaptive advantage, since in natural environments the food has a patchier distribution, thus determining the degree of association among snails and aquatic plants.

ACKNOWLEDGMENTS

This work was funded by CONICET (Consejo Nacional de Investigaciones Científicas y Técnicas), Argentina: P.I.D. #3688/92.

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Concholepas Lamarck, 1801 (Neogastropoda: Muricoidea): A Neogene Genus Native to South America

by

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Abstract. New discoveries of *Concholepas kieneri* Hupé, 1854, in Upper Miocene and Pliocene strata, and *C. nodosa* Möricke, 1896, in upper Pliocene strata of the Pisco Basin (south-central Peru), and *C. concholepas* (Bruguière, 1789) in lower Pleistocene beds of the Talara Basin (northernmost Peru) represent significant temporal and/or geographic range extensions of known species of the genus *Concholepas* Lamarck, 1801. A new middle Miocene species from the Pisco Basin, *C. unguis*, resembles some rapanine species. Shell morphology, paleoecology, and evolutionary timing suggest that the suite of South American species constitutes an endemic lineage and that non-South American species assigned to *Concholepas* are not closely related taxa.

INTRODUCTION

The genus *Concholepas* Lamarck, 1801, includes one living species, *Concholepas concholepas* (Bruguière, 1789), found in the cold-water Peruvian and Magellanic Provinces of western South America. Pliocene species of *Concholepas* have been recognized in Chile (Philippi, 1887; Möricke, 1896; Herm, 1969), but no older records of the genus have been reported from South America, nor have any fossil species been found that might suggest a relationship to other muricid taxa. Efforts to relate the heavy-shelled, shallow-water, Recent *Concholepas* from South America to thin-shelled, deep-water, early Neogene *Lippistes* from New Zealand (Beu, 1970) or to equally ancient taxa from France (Rambur, 1862) and Florida (Vokes, 1972) have not been persuasive. The genus has remained an evolutionary and biogeographic enigma.

This paper presents the first account of *Concholepas* from middle and upper Miocene strata of western South America. It includes a description of *C. unguis* sp. nov., a morphologically intermediate form with some characteristics of such modern rapanine taxa as *Vasula* Morch, 1861, and *Dicathais* Iredale, 1936. This paper also documents the Neogene distribution of *Concholepas* in Peru, where pre-Pleistocene occurrences of the genus had been unknown, and describes the northernmost occurrence of *Concholepas* near Cabo Blanco, Peru (4°15'S).

PREVIOUS STUDIES

The genus *Concholepas* has been assigned to the muricid subfamily Thaidinae Jousseaume, 1888, by Cooke (1919),

Stuardo (1979), and Kool (1987, 1989), usually on the basis of radular characteristics. More recently, Kool (1993) has assigned *Concholepas* to his redefined Rapaninae Gray, 1853, based on anatomy, radulae, and shell morphology.

The shell of *Concholepas concholepas* is large (typically 80–130 mm long and 60–90 mm wide) and robust, with a broadly elliptical aperture whose breadth and extension beyond the spire reflect a rapid rate of whorl expansion (Mabille, 1886; Carcelles, 1954). When the shell is oriented in life position, the pseudumbilical area forms a nearly vertical wall equal to half the dorso-ventral thickness of the shell. The pseudumbilicus is bordered by an arching, cordate, fasciolar ridge that wraps posteriorly behind a straight or recurved parietal flange.

The exterior of the shell is coarsely sculpted with about 10 primary spiral cords and two to four secondary cords in each of the interspaces. The spiral sculpture is intersected in well-preserved specimens by 30–40 small frilled axial costae on the body whorl. The spire is nearly involute on some specimens. Viewed from the ventral side, the spire's axis is rotated clockwise from the long axis of the body whorl.

Concholepas concholepas has been reliably reported from the Peruvian island of Lobos de Afuera (6°27'S) (Sanchez Romero, 1973) to Cape Horn (Stuardo, 1979). This author has encountered late Holocene specimens on the mainland as far north as Salaverry (8°10'S). Populations also occur on the Juan Fernandez Islands, 600 km west of Chile at about 34°S (Stuardo, 1979).

Accounts of *C. concholepas* collected from Mexico (v. Martens, cited in Dall, 1909) are probably in error, as

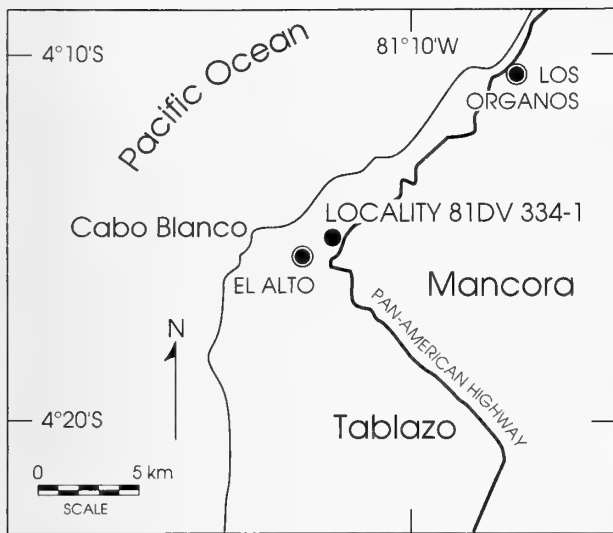


Figure 1

Map showing one locality (81DV 334-1) from which an early to middle Pleistocene specimen of *Concholepas concholepas* was collected near Cabo Blanco, northern Peru. Locality 81DV MT (see text) is from an unknown site on the surface of the Mancora Tablazo.

are accounts of the species in the Falkland (Malvinas) Islands (Gmelin, 1791), according to Carcelles (1954), who for many years vainly sought examples of *C. concholepas* in the Atlantic Ocean. However, the species has been found in Late Pleistocene middens along the South African coast (Kensley, 1985), demonstrating that populations of this planktotrophic species (Gallardo, 1973, 1979; Castilla & Cancino, 1976) can become established far from the South American mainland.

Concholepas concholepas is known to occur in Pleistocene marine-terrace deposits of Chile (Herm, 1969). Two extinct species, *Concholepas kieneri* Hupé, 1854, and *C. nodosa* Möricke, 1896, have been found in Pliocene deposits along the Chilean coast. The former species is less coarsely sculptured and more fusiform than *C. concholepas*, whereas the latter is more coarsely ornamented with spiral cords, broad smooth interspaces, and axial lamellae. Stuardo's (1979) assignment of an age of 10 million years to *C. kieneri* is based on an outdated definition of the Pliocene/Miocene boundary.

Long before much was known of fossil *Concholepas* in South America, Rambur (1862a, b) described a new middle Miocene species, *C. deshayesi*, from the Loire Basin of France. Tate (1894) described a middle Miocene (not Eocene; see Beu, 1970) species, *C. antiquata*, from Australia. More recently, Beu (1970) reassigned a Miocene New Zealand gastropod, *Lippistes pehuensis* Marwick, 1926, to the genus *Concholepas*. Soon thereafter, Vokes (1972) described a new late early Miocene species, *C. drezi*, from the Chipola Formation of Florida.

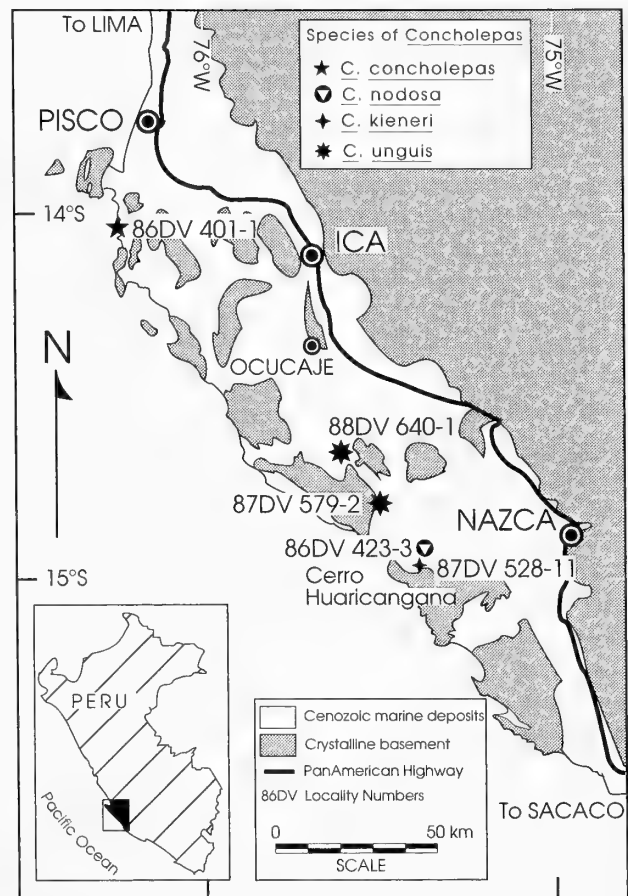


Figure 2

Map of the Pisco Basin, showing outcrops of basement and approximate localities from which specimens of four *Concholepas* species were collected.

GEOLOGY

Fossil and Recent specimens for this study were collected between 1981 and 1988 from the Talara Basin of northern Peru (Figure 1) and Pisco Basin and Sacaco Sub-basin of south-central Peru (Figures 2, 3). These are emergent forearc basins lying between the Peru-Chile Trench and the Andean Cordillera (Thornburg & Kulm, 1981). Post-Eocene bioclastic, shelf and marine-terrace sediments of the Talara Basin have been described by DeVries (1986, 1988). The stratigraphy of diatomaceous and tuffaceous sediments in the Pisco Basin has been detailed by Marocco & de Muizon (1988), Macharé et al. (1988), and Dunbar et al. (1990). The geology and paleontology of the Sacaco Sub-basin is discussed by de Muizon & DeVries (1985).

Geological data presented here were developed by this author unless noted otherwise. Ages based on the diatom zonation of Barron (1985) were provided by J. Barron (see also Macharé & Fourtanier (1987)) and H. Schrader (University of Bergen, Norway), using samples of marine diatoms collected from the Pisco Basin and Sacaco Basin.

by Schrader, J. Macharé, and this author. ^{39}Ar - ^{40}Ar radiometric ages were provided by L. Snee (U.S. Geological Survey, Boulder, Colorado). Other age determinations are based on a comparison of Peruvian molluscan assemblages with molluscan faunas of Chile (Philippi, 1887; Herm, 1969; Tavera, 1979).

Abbreviations used for localities or specimens are as follows: USNM: Department of Paleobiology, United States National Museum, Washington, D.C., USA; OSU: Orton Museum, Ohio State University, Columbus, Ohio, USA; L: Anterior-posterior Length; W: Width at widest point, perpendicular to length; THK: Dorso-ventral thickness, measured at widest point.

Material is described with a collections number, locality number, and dimensions (L, W, THK). Measurements enclosed by parentheses indicate sizes for broken specimens. Locality descriptions are given in the appendix.

SYSTEMATIC PALEONTOLOGY

Family MURICIDAE Rafinesque, 1815

Subfamily RAPANINAE Gray, 1853

Genus *Concholepas* Lamarck, 1801

Concholepas Lamarck, 1801:69.

Type species (monotypy).—*Concholepas peruviana* Lamarck, 1801 (= *Buccinum concholepas* Bruguière, 1789).

Diagnosis: Shell 30–120 mm long, length: width ratio about 1.2:1, moderately thick, ovate with no anterior constriction; spire rotated clockwise relative to axis of body whorl (viewed from ventral side); sutures usually appressed; aperture broad, 80–100% of shell length; inner lip deeply excavated; columella flattened, flattened surface twists into aperture; strong and elongate fasciolar ridge; very short siphonal canal; deep siphonal notch; sculpture of alternating primary and secondary spiral cords.

Concholepas concholepas (Bruguière, 1789)
(Figures 4, 6, 8, 9, 11, 19)

Buccinum concholepas Bruguière, 1789, p. 252.

Purpura concholepas d'Orbigny, 1841, v. 5, p. 437–438; v. 9, pl. 61, figs. 5–7.

Concholepas concholepas (Bruguière). Dall, 1909, p. 168, pl. 22, fig. 1; Carcelles & Williamson, 1951, p. 291; Carcelles, 1954, p. 268–271, pl. 4, figs. 1–11 (with synonymy through 1940); Herm, 1969, p. 136–137, pl. 18, figs. 4a, 4b; Beu, 1970, p. 44, pl. 4, figs. 10–12; Dell, 1971, p. 210–211; Vokes, 1972, Text-figure 2; Marinovich, 1973, p. 35, fig. 73; Stuardo, 1979, p. 10–12, pl. 1, figs. 1–8 (with extensive synonymy).

Concholepas peruviana Lamarck, 1801, p. 69.

?*Concholepas concholepas fernandezianus* Stuardo, 1979, p. 35–36, pl. 2, figs. 9–16, pl. 3, figs. 18–24.

Type Locality: Peru.

Material: OSU 37496, 81DV 334-1, L 78.6 mm, W (59.0) mm, THK (32.5) mm; OSU 37497, 81DV MT, L 76.8

mm, W (62.1) mm, THK (37.0) mm; USNM 447091, Lomas Trash, L 125.9 mm, W 96.9 mm, THK 65.1 mm; USNM 447092, Lomas Trash, L 99.1 mm, W 83.8 mm, THK 48.8 mm; USNM 447100, Lomas Trash, L 90.2 mm, W 74.5 mm, THK 41.4 mm; USNM 447101, 86DV 401-1, L 35.8 mm, W 25.9 mm, THK 13.8 mm; USNM 447109, 86DV 381-5, L 51.7 mm, W (38.7 mm), THK 22.1 mm.

Discussion: Two specimens of *C. concholepas* were discovered in 1981/1982 north of Talara, Peru (Figure 1). One specimen, collected from bioclastic sandstones of the Mancora Tablazo (OSU 37497), has a latest Pliocene or earliest Pleistocene age. The second specimen (OSU 37496) was recovered from a coquina at the base of a terrace intermediate in elevation between the Mancora and Talara Tablazos, which suggests an early to middle Pleistocene age (DeVries, 1988). The Talara occurrences constitute the northernmost occurrences of the genus for any epoch.

Variation within living populations of *Concholepas concholepas* (Schwabe, 1959; Lozada et al., 1976) exceeds that existing between fossil and Recent specimens. Late Pliocene/early Pleistocene specimens of *C. concholepas* from northern Peru resemble neither of the Pliocene species.

Occurrence: Uppermost Pliocene to middle Pleistocene (Mancora Tablazo, northern Peru; marine terraces, south-central Peru to Chile). Upper Pleistocene (marine terraces, south-central Peru to Chile). Holocene (Isla Lobos de Afuera (north-central Peru) to Cape Horn; South Africa; Juan Fernandez Islands).

Concholepas kieneri Hupé, 1854
(Figures 5, 10, 12, 13–16, 21, 22, 25)

Concholepas kieneri Hupé, 1854, v. 8, p. 203; Conq., pl. 3, figs. 4, 4a; Philippi, 1887, p. 55, pl. 6, fig. 1; Stuardo, 1979, p. 21, figs. 20, 22, 25; de Muizon & DeVries, 1985, p. 557, pl. 2, fig. e.

Concholepas nodosa Möricke, 1896; Herm, 1969, pl. 18, fig. 3; Stuardo, 1979, figs. 19, 21.

Type Locality: Coquimbo, Chile.

Material: USNM 447086, 83DV 360-23, L 70.1 mm, W 50.3 mm, THK 27.6 mm; USNM 447087, 83DV 362-6, L 61.7 mm, W 41.8 mm, THK 27.8 mm; USNM 447088, 38DV 361-6, L 102.2 mm, W 67.6 mm, THK 38.0 mm; USNM 447089, 83DV 361-6, L (45.8) mm, W 31.9 mm, THK 16.4 mm; USNM 447090, 88DV 528-11, L 69.0 mm, W 44.8 mm, THK 29.7 mm; USNM 447093, 87DV 562-10, L 57.6 mm, W 42.8 mm, THK 22.0 mm; USNM 447094, 83DV 360-1, L (29.4) mm, W 20.5 mm, THK 12.0 mm; USNM 447095, 87DV 562-4, L (42.7) mm, W 29.1 mm, THK 16.8 mm; USNM 447103, 83DV 370-1, L (74) mm, W 68.2 mm, THK (44) mm; USNM 447104, 83DV 370-1, L (65.5) mm, W (52) mm, THK (28) mm; USNM 447105, 83DV 360-23, L 27.6 mm, W 18.4 mm, THK 9.6 mm; USNM 447106, 83DV 361-6, L 49.1 mm,

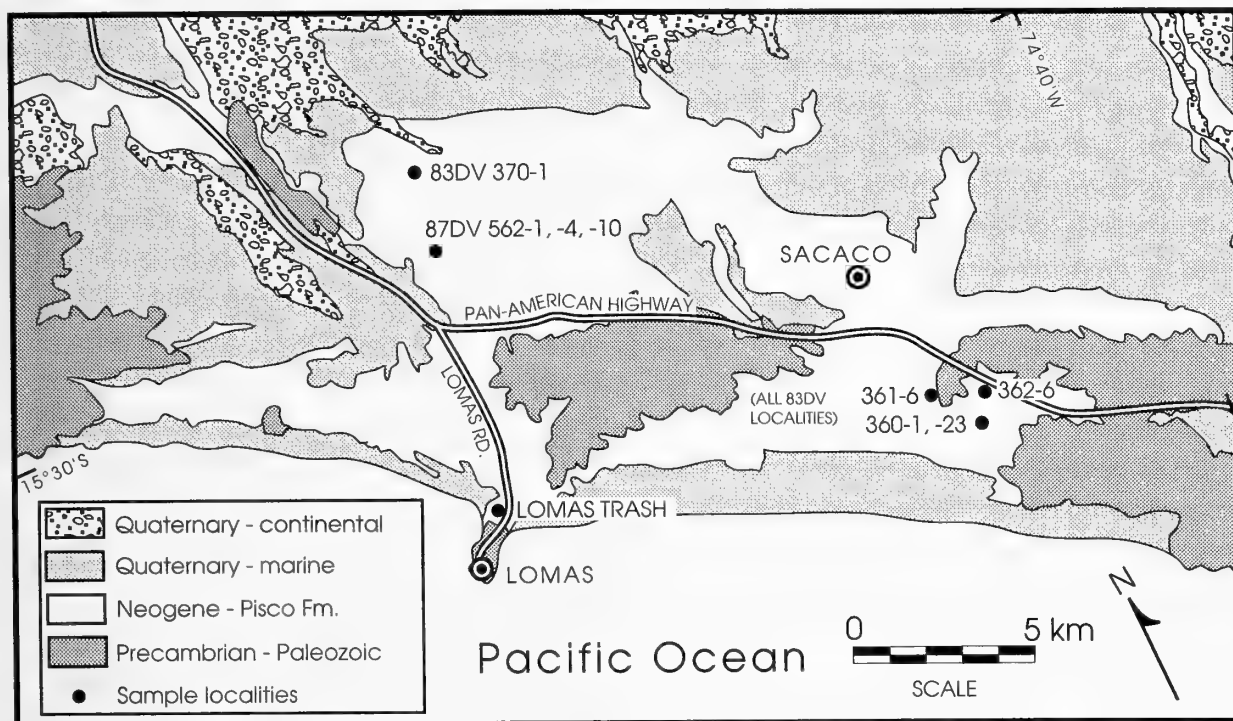


Figure 3

Geological map of the Sacaco Sub-basin, south-central Peru, showing Miocene and Pliocene localities with *Concholepas kieneri*. Geology after de Muizon & DeVries (1985).

W (34.5) mm, THK 15.8 mm; USNM 447107, 83DV 361-6, L (42.7) mm, W 34.5 mm, THK (21.5) mm.

Discussion: Specimens of *C. kieneri* from the Pisco Basin and Sacaco Sub-basin closely resemble specimens from Chile. No consistent differences were noted between Miocene and Pliocene specimens from Peru.

Occurrence: Upper Miocene (Pisco Formation, Peru). Pliocene (Pisco Formation, Peru; La Cueva Formation, Chile).

Concholepas nodosa Möricke, 1896
(Figure 7)

Concholepas sp. Philippi, 1887, p. 55, pl. 58, fig. 12.

Concholepas nodosa Möricke, 1896, p. 560, pl. 11, figs. 14, 15; Herm, 1969, *partim*, p. 137, pl. 18, fig. 1a, 1b, 2.

Type Locality: Coquimbo, Chile.

Material: USNM 447102, 86DV 423-3, L (106) mm, W (81) mm, THK (33) mm; USNM 447110, 86DV 423-3, L (47.7) W (44.8).

Discussion: *Concholepas nodosa* is represented by several specimens collected from a marine terrace that caps upper Miocene and lower Pliocene strata north of Cerro Huar-

icangana (Figure 2). The terrace deposit contains an unusual fauna composed of extinct Pliocene species and extant Quaternary species, suggesting a late Pliocene/early Pleistocene age.

Stuardo (1979) rightly pointed out the confusion created by Herm (1969), who presented a figure of *C. kieneri* under the name of *C. nodosa*, and by Möricke (1896), who named *C. nodosa* after a juvenile character that is more evident in specimens of *C. kieneri*. Stuardo (1979) further muddled the waters, however, by suggesting that examples of *C. kieneri* with more pronounced nodules on the primary spiral cords (Stuardo, 1979; Figures 19, 21) may be examples of *C. nodosa*.

A comparison of equally small specimens of *C. kieneri* (USNM 447105) and *C. nodosa* (Möricke, 1896: pl. 11, figs. 14, 15) shows that while nodular primary spiral cords occur in both species, the smoother and broader interspaces of the latter species clearly distinguish it from *C. kieneri*, specimens of which have interspaces scored by secondary spiral cords. In larger specimens, such as those figured by Herm (1969), Stuardo (1979), and herein, nodules evolve into coarse lamellae in *C. nodosa* but persist as nodules in *C. kieneri*.

Occurrence: Lower to upper Pliocene (lower and upper Series of Herm (1969) in Chile). Uppermost Pliocene (marine terrace, south-central Peru).

Concholepas unguis DeVries, sp. nov.

(Figures 17, 18, 20, 23, 24, 26)

Diagnosis: Shell small for the genus with low to moderately elevated spire; fasciolar ridge pronounced; pseudumbilical area narrow, extending only one-third length of shell; surface sculpture of alternating primary and secondary spiral cords of nearly equal strength.

Description: Shell small for the genus, not exceeding 30 mm; ovate, consisting of a broad body whorl (80–95% of the shell length) and usually short spire. Spire consisting of at least two to three whorls; protoconch unknown. Body whorl evenly convex, with no pronounced shoulder and periphery at midpoint of whorl. Anterior quarter of the body whorl faintly constricted; depression behind the fasciolar ridge absent or barely developed; fasciolar ridge strong; pseudumbilical area usually as narrow as fasciolar ridge, extending for less than one-third of shell length. Inner lip excavated, columella slightly thickened and flattened; outer lip moderately thick, with internal crenulations or dentition not visible. Siphonal canal short. Anal sulcus small to non-existent. Surface sculpture consisting of about 13 primary, flattened spiral cords and an equal number of secondary spiral cords, nearly equal in size. Axial sculpture consisting of regular, slightly scalloped and scaly growth lines.

Discussion: The broad, uniformly convex body whorl, long and broad aperture, and strong fasciolar ridge are similar to those of larger specimens of late Miocene *Concholepas kieneri* from the same basin. Moreover, the coiling axis of the body whorl is rotated relative to the axis of the spire in the same clockwise manner as that of more recent species of *Concholepas*.

Specimens of *Concholepas unguis* do not resemble specimens of contemporaneous South American *Acanthina* Fischer von Waldheim, 1807, which have heavier shells and

thickened outer lips with a strong labial tooth and associated groove on the body whorl. Specimens of *C. unguis* also differ from Miocene and Pliocene specimens belonging to the muricid genus *Chorus* Gray, 1847, which are distinctly fusiform or pear-shaped and, like specimens of *Acanthina*, have a prominent labial tooth and groove on the body whorl.

No published figures of Chilean mesogastropods resemble *C. unguis* except that of *Fusus sulcatus* (Nobilis in Hupé, 1854). Hupé's specimen shares similar apertural and sculptural traits with *C. unguis* but seems to be more fusiform. The location of Hupé's type specimens is at present unknown (D. Frassinetti, personal communication, August, 1993). No specimens comparable to *C. unguis* were found in collections of the Museo Nacional de Historia Natural (Santiago, Chile) or in collections of J. Tavera at the Universidad de Chile.

The form of *C. unguis*—broad aperture, short spire, excavated inner lip—resembles that of the modern *Vasula melones* (Duclos, 1832), a rapanine species from the eastern Pacific Ocean. In contrast to *V. melones*, the fasciolar ridge of *C. unguis* is more elongate and the coiling axis of the spire is rotated clockwise. Also, larger specimens of *C. unguis* are dorso-ventrally flattened, as in specimens of late Miocene *C. kieneri*.

Type Locality: 14°46'30"S, 75°30'06"W (Lomitas 1:100,000 quadrangle); 2 km NW Fundo Santa Rosa, in hills east of the Río Ica (Figure 27), about 200 m east of road going to coast, in thin beds of coarse-grained bioclastic sandstone with associated boulders of basement rock (Locality 87DV 579-2). Also found nearby in coarse-grained sandstone horizons within medium-grained and fine-grained tuffaceous sandstone sequences at Cerro Sechuita, east of the Río Ica (Locality 88DV 640-1).

At its type locality, *Concholepas unguis* occurs in an indurated coarse-grained sandstone just above a horizon containing scattered sub-angular boulders of basement rock.

Explanation of Figures 4 to 12

Figures 4, 6, 8, 9, 11. *Concholepas concholepas* (Bruguière, 1789).

Figure 4. USNM 447092. Lomas Trash, south-central Peru. Recent. Ventral view showing spire entirely above plane of aperture ($\times 0.75$).

Figure 6. USNM 447092. Dorsal view showing rotation of spire relative to body whorl ($\times 0.75$).

Figure 8. OSU 37496. Locality 81DV 334-1, terrace between Mancora and Talara Tablazos, northern Peru. Early to middle Pleistocene. Dorsal view. Posterior portion of outer lip is broken, as is spire ($\times 0.95$).

Figure 9. USNM 447109. Locality 86DV 381-5, San Juan-Lomas road terrace. Middle Pleistocene. Ventral view. Outer lip broken ($\times 1.00$).

Figure 11. OSU 37497. Locality 81DV MT, Mancora Tablazo,

northern Peru. Early Pleistocene. Dorsal view, internal sandstone cast ($\times 0.85$).

Figures 5, 10, 12. *Concholepas kieneri* Hupé, 1854.

Figure 5. USNM 447094. Locality 86DV 360-1, South Sacaco. Early Pliocene. Ventral view ($\times 1.52$).

Figure 10. USNM 447088. Locality 83DV 361-6, South Sacaco. Early Pliocene. Ventral view showing minor encroachment of spire across plane of aperture ($\times 0.75$).

Figure 12. USNM 447088. Ventral view ($\times 0.75$).

Figure 7. *Concholepas nodosa* Möricke, 1896. USNM 447110, Locality 86DV 423-3, Quebrada Huaricangana. Late Pliocene. Fragment of body whorl and outer lip showing frilled spiral cords and wide interspaces ($\times 0.88$).



4



5



6



7



8



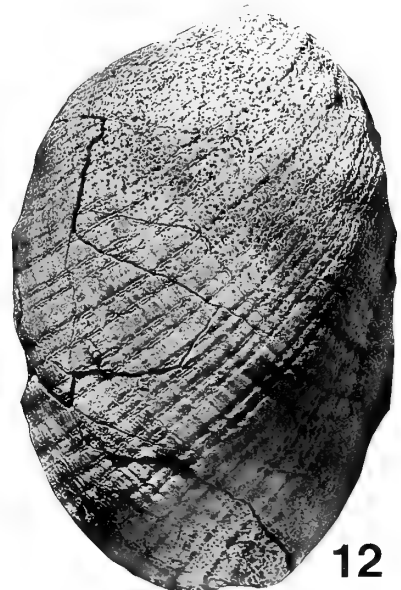
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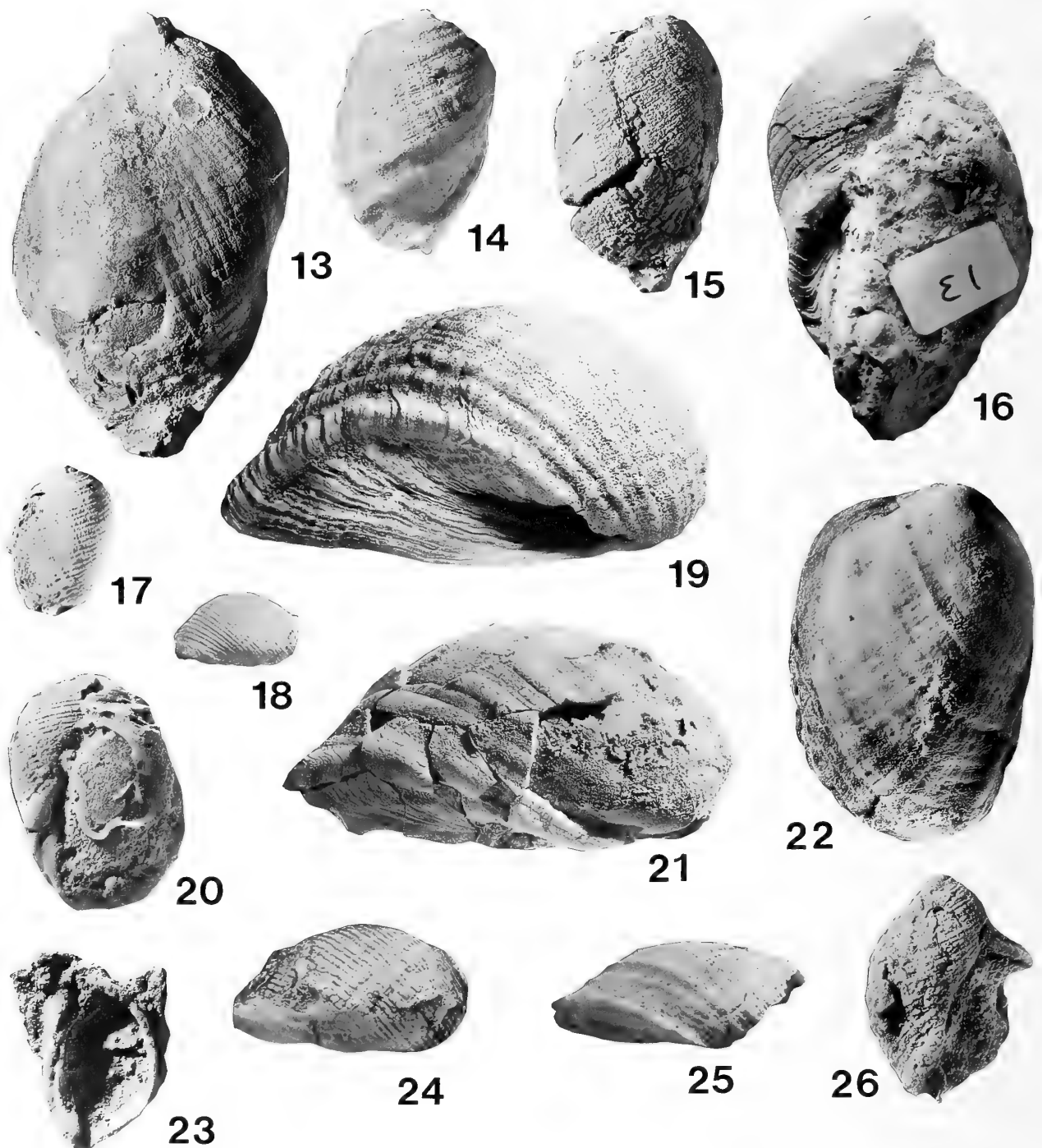
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12



Explanation of Figures 13 to 26

Figures 13-16, 21, 22, 25. *Concholepas kieneri* Hupé, 1854.

Figure 13. USNM 447090. Locality 88DV 528-11, Quebrada Huaricangana, late Miocene/early Pliocene. Dorsal view showing elongate spire. Spire represented by internal cast ($\times 1.03$).

Figure 14. USNM 447105. Locality 83DV 360-23, south Sacaco. Early Pliocene. Dorsal view of juvenile specimen showing small nodes on primary cords ($\times 1.42$).

Figure 15. USNM 447095. Locality 87DV 562-4, Aguada de Lomas. Late Miocene. Dorsal view ($\times 1.03$).

Figure 16. USNM 447090. Ventral view showing atypically narrow aperture ($\times 1.03$).

Figure 21. USNM 447103. Locality 83DV 370-1, Aguada de Lomas, late Miocene. Lateral view showing modest breadth of pseudumbilical area. Spire represented by internal cast ($\times 1.16$).

The boulder bed lies about 30 m above another horizon with basement boulders. The two beds, regarded as disconformities, also occur to the north at Quebrada Gramonal and to the northwest on the west side of the Río Ica (Figure 27). Diatoms collected from tuffaceous siltstones 40 m above the second boulder bed west of the Río Ica yield middle Miocene ages (P. Rønning, 1990, unpublished MS thesis, University of Bergen, Norway), consistent with an ^{39}Ar - ^{40}Ar age of 9.22 my for an ash bed slightly higher in the section (Snee, written communication, 1990). Rønning also reports late early Miocene to early late Miocene ages for diatomaceous siltstones between the two boulder beds. Thus, the evidence from west of the Río Ica indicates an early middle Miocene age for *C. unguis* at Locality 87DV 579-2. At locality 89DV 640-1, no microfossils were collected, but the occurrence of *C. unguis*-bearing strata below upper Miocene tuffaceous siltstones and above a regional boulder-strewn unconformity is consistent with a middle Miocene age.

Etymology: "unguis" = nail. The size, shape, and texture of this species recall a thumb and thumbnail.

Material: Holotype USNM 447096, 87DV 579-2, L 25.0 mm, W 19.5 mm, THK 12.3 mm; Paratype USNM 447108, 87DV 579-2, L 15.2 mm, W (10.6) mm, THK 8.2 mm. Referred specimens: USNM 447097, 89DV 640-1, L 20.3 mm, W (12.0) mm; USNM 447098, 89DV 640-1, L (26.2) mm, W (19.6) mm; USNM 447099, 89DV 640-1, L (20.2) mm, W (17.2) mm.

Occurrence: Middle Miocene (Pisco Formation, south-central Peru).

DISCUSSION

Distribution

An understanding of the paleobiogeography and paleoecology of *Concholepas* in South America is hindered by the uneven level of study of Neogene mollusks in South America. Whereas the efforts of Chilean paleontologists have led to a modestly detailed account of Miocene and

Pliocene mollusks in central and southern Chile, sporadic research to the north has resulted in a much less complete picture in northern Chile and Peru. Only the molluscan faunas of the Sechura and Talara Basins of northernmost Peru have received as close scrutiny as those of Chile (Olsson, 1932; DeVries, 1986, 1988). Thus, present discoveries of *Concholepas* in south-central Peru fill a significant gap in our knowledge of the genus.

Concholepas unguis has been found only in south-central Peru, in deposits attributable to inner shelf and shallow subtidal environments, based on sedimentological characteristics (ripple marks, crossbedding, coarse-grained sands) and stratigraphic proximity to boulder-containing disconformities (Locality 87DV 579-2) and basement outcrops (Locality 89DV 640-1). The former locality may be as old as late early Miocene and the latter locality, as young as early late Miocene, but a conservative interpretation of the radiometric and micropaleontological data suggests a probable middle Miocene age. A seeming lack of similarly aged strata in Chile (Tavera, 1979) and limited collecting from Miocene strata in the Sechura Basin of northern Peru (Olsson, 1932) may explain the scarcity of records of early Neogene *Concholepas*.

Discoveries of *Concholepas kieneri* in bioclastic beach deposits adjacent to basement outcrops near Sacaco (de Muizon & DeVries, 1985) extend the range of the species northward by 1500 km. The Sacaco *Concholepas* horizons underlie tuffaceous beds radiometrically dated at 3.9 my (de Muizon & Bellon, 1980; de Muizon & DeVries, 1985) and lie between diatomaceous tuffaceous siltstones dated as early Pliocene (Schrader, written communication, 1986).

Late Miocene occurrences of *C. kieneri* constitute the oldest records of the species in Peru or Chile. Fragments of *C. kieneri*, which are abundant in aprons of bioclastic coquina surrounding former basement stacks near Ocucaje (Figure 2), are between 5 and 7 my old, based on the co-occurrence in laterally contiguous tuffaceous siltstones of the diatoms *Thalassiosira antiqua* and *Rosielia tatsunokuchiensis* (Schrader, written communication, 1986) and ^{39}Ar - ^{40}Ar ages of less than 7 my (Snee, written communication, 1990). Late Miocene/Pliocene (*Thalassiosira convexa*

Figure 22. USNM 447093. Locality 87DV 562-10, Aguada de Lomas. Late Miocene. Dorsal view ($\times 0.98$).

Figure 25. USNM 447105. Lateral view of juvenile specimen. Spire and ventral portion of body whorl broken ($\times 1.48$).

Figure 19. *Concholepas concholepas* (Bruguière, 1789). USNM 447092. Lateral view showing fasciolar ridge and broad pseudumbilical area ($\times 0.75$).

Figures 17, 18, 20, 23, 24, 26. *Concholepas unguis* DeVries, sp. nov. All middle Miocene.

Figure 17. USNM 447108. Paratype. Locality 87DV 579-2, near Fundo Santa Rosa. Dorsal view ($\times 1.59$).

Figure 18. USNM 447108. Lateral view of juvenile specimen ($\times 1.38$).

Figure 20. USNM 447096. Holotype. Locality 87DV 579-2, near Fundo Santa Rosa. Ventral view. Aperture mostly obscured ($\times 1.53$).

Figure 23. USNM 447097. Locality 640-1, Cerro Sechuita. Ventral view. Spire and dorsum obscured and/or broken ($\times 1.53$).

Figure 24. USNM 447096. Lateral view showing short and narrow pseudumbilical area ($\times 1.53$).

Figure 26. USNM 447098. Locality 88DV 640-1, Cerro Sechuita. Ventral view. Outer lip and siphonal canal broken ($\times 1.41$).

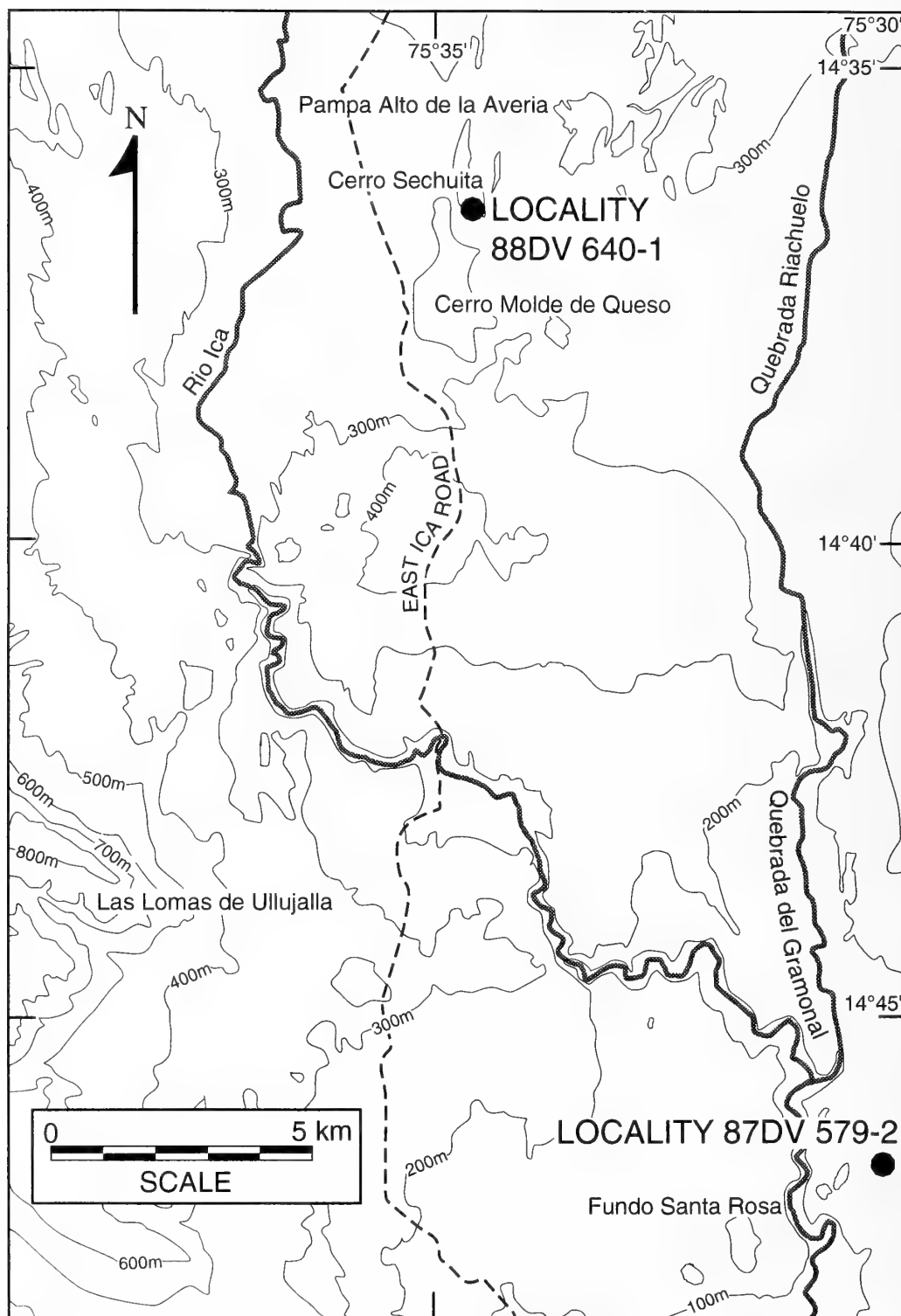


Figure 27

Type locality (87DV 579-2) and a second locality in the Pisco Basin with *Concholepas unguis* DeVries, sp. nov. Topography and landmarks are adapted from Lomitas 1:100,000 quadrangle map.

"subzone c" and slightly younger, according to H. Schrader, written communication, 1987) specimens of *C. kieneri* also are found in alluvial fanglomerates on the northern wall of Cerro Huaricangana. Specimens from the Sacaco Sub-Basin, at Aguada de Lomas, are found 50–100 m above ash beds dated at 8.8 and 8.0 my (de Muizon & Bellon, 1980; de Muizon & DeVries, 1985).

Specimens of *Concholepas nodosa* occur in a terrace deposit at an elevation of 650 m above sea level on the north side of Quebrada Huaricangana (Figure 2). A late Miocene age for underlying tuffaceous siltstones and mollusks from interbedded sandstone horizons is indicated by microfossils and mollusks. The occurrence of mollusks in the terrace deposit known in the region only since the Pleistocene (DeVries, 1986), together with species previously known only from the Pliocene of Chile (Herm, 1969), suggests a latest Pliocene/earliest Pleistocene age for the terrace fauna.

No examples of *Concholepas* have been reported from upper Miocene beds within the Sechura Basin or in Miocene deposits of the Zapallos Formation of northern Peru, nor have any been discovered in Pliocene beds of the Hornillos Formation of the Sechura Basin. So little effort has been devoted to collecting mollusks from the Sechura Basin (Olsson, 1932; Zuniga y Rivero, 1970; DeVries, 1986), however, that at present little significance can be attached to the late Miocene or Pliocene northern range limit of *Concholepas*.

An examination of Tertiary mollusks in the collections of the Museo Nacional de Historia Natural (Santiago, Chile) and the collections of J. Tavera of the Universidad de Chile in 1993 uncovered no specimens of *Concholepas* from upper Miocene strata of Chile.

Based on what is currently known of the distribution of South American *Concholepas*, it appears that the genus has been represented by a single species (during the Pliocene, two species) within the modern limits of the Peruvian Province from the middle Miocene onwards. *Concholepas concholepas*, which appeared in the intertidal realm at the onset of the Pleistocene Epoch, has shown a great capacity for dispersal in the cooler southern oceans as well as the once-cooler waters of northern Peru (DeVries, 1986).

Evolution

The point at which the fasciolar ridge rises dorsally above the plane of the aperture in specimens of *Concholepas* exhibits a posterior migration progressively from the middle Miocene (*C. unguis*) to late Miocene/Pliocene (*C. kieneri*) to late Pliocene (*C. nodosa*) to Pleistocene (*C. concholepas*). The resulting posterior elongation of the pseudumbilicus in *C. kieneri* was accompanied by dorsal-ventral compression of the body whorl with no anterior constriction. Consequently, the ventral part of the body whorl barely projected downward through the plane of the aperture, allowing more of the aperture's perimeter to press

directly against the substrate. Such a configuration might have enabled individuals to better withstand predation or wave impacts on rock surfaces.

The compressed shell of *C. kieneri* seems to have proved weaker as shell size increased after the middle Miocene and as the axial cross-sectional profile became increasingly rectangular in response to the posterior migration of the fasciolar ridge and the modest broadening of the pseudumbilical area. Circumstantial evidence of structural weakness is provided in the illustrations of Stuardo (1979) and by observations of this author, which indicate that shells of *C. kieneri* are more likely to be broken on the dorsal face of the body whorl than are shells of *C. concholepas* or *C. unguis*.

The first adaptation resulting in a stronger shell for *Concholepas* probably was the development of coarse, lamellose, primary cords in specimens of *C. nodosa*, which otherwise remained dorso-ventrally compressed. The inflated body whorl in specimens of *C. concholepas* may have constituted a subsequent and more successful adaptation for strength. Simultaneously, an extreme broadening of a very long pseudumbilical area lifted the newly evolved inflated whorls above the plane of the aperture, thereby retaining a complete seal between aperture and substrate.

Discussions of *Concholepas* evolution have been predicated on the assumption that worldwide, fossil species originally or subsequently assigned to the genus on the basis of ostensibly shared derived characters (flaring aperture, low or submerged spire, and strong fasciolar ridge, according to Beu (1970), Vokes (1972), and Stuardo (1979)) are indeed related. Discoveries in Peru of *C. kieneri* in lower upper Miocene sandstones and a morphologically primitive *Concholepas* species in middle Miocene sandstones require that the evolutionary history of *Concholepas* be re-evaluated. This can be accomplished by examining the morphological and ecological similarities and dissimilarities of South American and non-South American species assigned to *Concholepas* (Table 1).

Shape

Length/width (L/W) ratios of *Concholepas concholepas* average about 1.25; for *C. nodosa* and *C. kieneri*, about 1.40; and for *C. unguis*, about 1.3. All fossil specimens of "*Concholepas*" species found outside of South America have L/W ratios less than or very close to 1.0 (Stuardo, 1979). Two corrections regarding the ratios must be noted. First, the published length and width of the holotype of *Lippistes pehuensis* cited in Beu (1970) are reversed, an error that was perpetuated by Stuardo (1979). Figs. 1 and 3 in Beu's pl. 4 clearly show a L/W ratio of less than 1.0. A L/W ratio measured from the figures (0.804) is the same as one calculated from the published values of height and width, if the values are switched. Secondly, the smaller specimen of "*Concholepas*" *antiquata* figured by Beu (1970; pl. 4, figs. 7–9) has a broken outer lip. With the lip restored,

Table 1

Comparison of shell characteristics of species of *Concholepas* (Lamarck, 1801) and other species previously assigned to *Concholepas*.

Species	L:W ratio	Spire form and position relative to posterior edge of aperture	Body whorl rotation	Sutures	Shell wall thickness	Anterior constriction	Fasciolar ridge	Pseudumbilical area	Posterior notch
<i>Concholepas concholepas</i>	1.25	Submergent, slightly anterior	Moderate	Broadly impressed	Thick	No	Strong	Broad	No
<i>Concholepas nodosa</i>	1.4	Submergent, slightly anterior	Moderate	Broadly impressed	Thick	No	Strong	Mod. wide	No
<i>Concholepas kieneri</i>	1.4	Submergent, even or posterior	Moderate	Appressed	Mod. thick	No	Strong	Narrow	No
<i>Concholepas unguis</i>	1.3	Fusiform, posterior	Slight	Appressed	Mod. thick	No	Strong	Very narrow	No
<i>Lippistes pehuensis</i>	0.8	Submergent, nearly medial	Great	Mod. impressed	Thin	Yes	Weak	Broad	Weak
" <i>Concholepas</i> " <i>deshayesi</i>	1.06	Submergent, nearly medial	Great	Deeply impressed	Thin	No	Strong	Broad	No
" <i>Concholepas</i> " <i>drezi</i>	1.1	Slightly emergent and anterior	None	Deeply impressed	Thin	Yes	Strong	Broad	No
" <i>Concholepas</i> " <i>antiquata</i>	1.0	Submergent and anterior	None	Deeply impressed	Thin	No	Strong	Broad	Strong

the L/W ratio would be much closer to the ratio of 1.0 exhibited by the larger specimen of "*C.*" *antiquata* (pl. 4, figs. 4–6).

Specimens of "*C.*" *drezi* and *Lippistes pehuensis* exhibit an anterior constriction of the body whorl. Specimens of South American species, "*C.*" *antiquata*, and "*C.*" *deshayesi* lack such an anterior constriction.

Spire and Sutures

The spire of *C. unguis* is invariably fusiform, although variably elongate. The spires of *C. kieneri* and *C. nodosa* are usually incipiently submergent or barely emergent, although in rare cases they are markedly fusiform (USNM 447090; Figures 13, 16). Only the spire of *C. concholepas* is typically submergent, but it is with this Quaternary species that non-South American Miocene species (all but "*C.*" *drezi* having submergent spires) are compared.

The spires of all South American species of *Concholepas* are located slightly anterior to, even with, or posterior to the posterior edge of an evenly rounded, non-flaring aperture. The figured holotypes of "*Concholepas*" *deshayesi* and *Lippistes pehuensis* show subdiscoidal coiling with the spires situated nearly medially. The spire of "*C.*" *drezi* is not so centrally located, although it still lies well below the posterior edge of the outer lip, which flares posteriorly and abapically. Only the spire of *L. pehuensis* is located in the same relative position as the spire of South American *Concholepas* species.

The spire in all South American species of *Concholepas* is slightly to moderately rotated in a clockwise direction relative to an axis that joins the siphonal notch with the

visible or inferred protoconch. This rotation results from a rapid expansion of the anterior portion of the body whorl. The spires in figured specimens of "*Concholepas*" *antiquata* and "*C.*" *drezi* shows no such rotation, whereas the spires in figured specimens of *L. pehuensis* and "*C.*" *deshayesi* show extreme rotation.

All specimens of *C. unguis*, some of *C. kieneri*, and the spire whorls on specimens of all South American species have appressed sutures. Sutures bordering the body whorls in most specimens of *C. kieneri* and all *C. concholepas* are broadly impressed. In contrast, the spires and body whorls of non-South American species have moderately to deeply impressed sutures.

Fasciolar Ridge and Pseudumbilical Area

The fasciolar ridge in specimens of all South American species of *Concholepas* is well developed, leading to a prominent though short siphonal notch. The pseudumbilical area in specimens of the oldest South American species (*C. unguis*, *C. kieneri*) is very narrow, whereas in the youngest species (*C. concholepas*), it is unusually wide. *Lippistes pehuensis* has a weak fasciolar ridge, poorly developed siphonal notch, and broad pseudumbilical area. "*C.*" *antiquata*, "*C.*" *drezi*, and "*C.*" *deshayesi* have fasciolar ridges comparable in strength and pseudumbilical areas comparable in size to the Recent South American species, *C. concholepas*.

Paleoecology

Specimens of the oldest known *Concholepas* from South America, *C. unguis*, were found in thin-bedded, coarse-

grained, bioclastic sandstones interbedded with massive, bioturbated, silty sandstones and thick sections of tuffaceous, sandy, diatomaceous siltstones thought to have been deposited close to shore. Similar sedimentological evidence at Aguada de Lomas (de Muizon & DeVries, 1985), where Upper Miocene sandstones contain whole specimens of *C. kieneri*, indicates that for most of the Miocene, *Concholepas* appears to have favored inner shelf, sandy-bottom environments.

Latest Miocene and Pliocene specimens of *Concholepas* in Peru occur together with other epibenthic muricids, trochids, and balanids in aprons of coquina and cobbly alluvium adjacent to former bedrock stacks and coastal promontories. No specimens of *Concholepas* of these ages were found in thin sandstone beds such as those that contain *Concholepas* of middle and earlier late Miocene age.

Late Pliocene specimens of *C. nodosa* and Quaternary specimens of *C. concholepas* are usually found in the bioclastic cobbly sandstones of marine terrace deposits (Herm, 1969). The diversity of rocky-intertidal epibionts and endobionts on *C. concholepas* and on the Peruvian specimens of *C. nodosa* (in contrast to the absence of epibionts and endobionts other than boring algae on specimens of older *Concholepas* species) and the heavier shells of these species suggests that latest Cenozoic populations were adapted to environments subject to higher wave energy than those occupied by their Pliocene or Miocene predecessors.

Middle Miocene Australasian and European species of "*Concholepas*" probably lived at inner to outer shelf depths, judging from the fine-grained sediments in which specimens are found or the molluscan species with which they are associated (Beu, 1970). Specimens of the early Miocene Floridian "*C.*" *drezi* were found close to a contemporaneous coral reef (Vokes, 1972). None of these older thin-shelled species appear equipped to survive in the violent intertidal zone inhabited by *Concholepas concholepas*, the modern species with which the non-South American species are compared.

CONCLUSIONS

New discoveries of four *Concholepas* species in southern and northern Peru establish the genus as a Neogene endemic element of Peruvian-Province molluscan faunas. Evidence suggests that the genus arose from a muricid ancestor during the early or early middle Miocene and with time adapted to progressively higher energy coastal environments. It seems simplest to view the extant species of the South American group, *C. concholepas*, as an example of morphological convergence with an unrelated collection of older deeper-water gastropods from elsewhere in the world. The taxonomic position of non-South American species once assigned to *Concholepas* now needs to be re-evaluated.

ACKNOWLEDGMENTS

I would like to thank D. Frassinetti, V. Covacevich, and H. Nuñez for their hospitality while working in Santiago,

Chile, and A. Beu for his advice and encouragement. Research leading to this article was funded by a Shell Doctoral Fellowship, National Science Foundation Grant EAR-85-03886, and the Conchologists of America, Inc.

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APPENDIX

LOCALITY LIST

- 81DV 334-1 2km NE El Alto. E end of ridge bounding S side of Army rifle range (no quadrangle maps available). 1-m thick balanid coquina at base of marine terrace intermediate in elevation between Mancora and Talara Tablazo.
- 81DV MT Indeterminate locality within the coquinas of the Mancora Tablazo, on plateau between El Alto and Los Organos.
- 83DV 360-1 15°34'43"S, 74°43'17"W; South Sacaco, NW face of ridge SW of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Bone bed with sandstone concretions at base of ridge.
- 83DV 360-23 15°34'43"S, 74°43'17"W; South Sacaco, NW face of ridge SW of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Two successive beds of calcareous sandstone and concretionary sandstone

- densely packed with valves of the pelecypods *Dosinia* and *Amiantis*.
- 83DV 361-6 15°34'17"S, 74°43'26"W; South Sacaco, NE rim of depression W of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Mollusk and barnacle beds on upper half of slope, NW of pinnacles of igneous rock.
- 83DV 362-6 15°34'25"S, 74°43'00"W; South Sacaco, E rim of depression W of PanAmerican Highway (Yauca Quadrangle 1:50,000, 1967). Beds of mollusks at mid-slope below short sandstone ledge by highway.
- 83DV 370-1 15°27'19"S, 74°49'8"W; Aguada de Lomas, NE corner of depression; N of "Hierro Road" (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Terrace ledge with abundant mollusks in sandstone.
- 86DV 381-5 15°22'59"S, 75°03'11"W; Ridge at km 47.5 along Lomas-San Juan road (San Juan Quadrangle 1:100,000). Coquina at top of ridge.
- 86DV 401-1 14°02'31"S, 76°15'51"W; Hueco La Zorra (Punta Grande Quadrangle 1:100,000, 1985), modern beach at north end, just E of first point.
- 86DV 423-3 14°55'33"S, 75°17'41"W; double-knobbed mesa N of Quebrada Huaricangana (Puerto Caballas Quadrangle 1:50,000). Mollusk bed capping S side of NE knob.
- 87DV 562-1 15°29'13"S, 74°48'16"W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Dosinia* just above cobble bed.
- 87DV 562-4 15°29'13"S, 74°48'16"W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Mulinia* 40 m upsection from 87DV 562-1.
- 87DV 562-10 15°29'13"S, 74°48'16"W; Aguada de Lomas (Llucyuca o Cueva Santa Quadrangle 1:50,000, 1967). Mollusk beds with *Mulinia* 200 m upsection from 87DV 562-1.
- 87DV 579-2 14°46'30"S, 75°30'06"W; 1 km E double knob downstream from Quebrada Gramonal, 2 km NE Fundo Santa Rosa (Lomitas Quadrangle 1:100,000). Broken-up area w/ diatomite; platey green siltstone; *Turritella* beds; basement blocks exposed intermittently.
- 88DV 528-11 14°57'47"S, 75°16'58"W; Third gulch from W, S side Quebrada Huaricangana (Palpa Quadrangle 1:100,000, 1986). Shelly beds at mid-section.
- 89DV 640-1 14°36'21"S, 75°34'41"W; South end Cerro Sichuita (Lomitas Quadrangle 1:100,000, 1977). Lower flank of hill between two north-south knobs.
- Lomas Trash Approximately 15°33'S, 74°50'W; trash heaps of *Concholepas concholepas* on W side of road to Lomas (Yauca Quadrangle 1:100,000, 1982).

The Misidentified Holotype of *Argopecten circularis* (Bivalvia: Pectinidae)

by

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Abstract. The holotype of the common Eastern Pacific scallop *Argopecten circularis* (G. B. Sowerby I, 1835) was misidentified as a new species by Sowerby. Rather, it is a specimen of the Western Atlantic Bay Scallop, *Argopecten irradians concentricus* (Say, 1822), accompanied by erroneous data saying that it came from the Gulf of California at Guaymas, Mexico. The holotype of *Pecten circularis* is illustrated herein for the first time and its tangled background discussed. The valid name of this common species should become *Argopecten ventricosus* (G. B. Sowerby II, 1842), a lectotype for which is designated and figured.

INTRODUCTION

The name *Argopecten circularis* (G. B. Sowerby I, 1835) has long been applied to the common Eastern Pacific species popularly known as the “Pacific Calico Scallop” (Abbott, 1974; Turgeon et al., 1988), the “Speckled Scallop” (Haaker et al., 1988), or, in Mexico, the “Catarina Scallop” (Felix-Pico, 1991). This species is common, locally abundant, and commercially important in Mexico, Panama, Colombia, and Ecuador and is currently the subject of efforts in aquaculture (Shumway, 1991; Shumway & Sandifer, 1991). The species has also been referred to frequently in the literature of paleontology (Moore, 1984, and references therein).

In 1977, I discovered that the type specimen of *Argopecten circularis* at the British Museum (Natural History) in London (now The Natural History Museum) is in fact a specimen of the common western North Atlantic bay scallop *Argopecten irradians concentricus* (Say, 1822). Aside from references to this discovery in the form of personal communications (e.g., Haaker et al., 1988:1, and Turgeon et al., 1988:26) and a brief footnote by Waller (1991:72), the full details have never been reported. Furthermore, although some authors (Grant & Gale, 1931:218; Grau, 1959:99) have indicated that the type specimen of “*Pecten*” *circularis* is in the collections of the British Museum, no one to my knowledge has published photographs of this specimen.

In the present study, the type specimen of *Pecten circularis* Sowerby I, 1835, is illustrated by photographs for the first time, and the type status of the specimen and its species identity are examined in detail. It will be argued

that the name should be replaced by the next available name, *Pecten ventricosus* G. B. Sowerby II, 1842, rather than be conserved by attempting to use the Plenary Powers of the International Commission on Zoological Nomenclature.

THE TYPE OF *PECTEN CIRCULARIS*

The specimen that is labeled as the holotype of *Pecten circularis* in The Natural History Museum, London, bears the registration number BMNH 1950.11.14.18–19. It consists of a pair of matching valves (Figures 1–4) with height 38.9 mm (measured from right beak to ventral margin), length 39.1 mm, and convexity 25.6 mm (measured across closed valves between points of highest convexity on each valve). There are 18 radial ribs on the disk of the left valve, and 17 on the right.

This specimen is clearly not in accord with the concept of “*Argopecten circularis*” as now applied to the well-known species that lives along the west coasts of the Americas (Figures 5–8). Rather, it is a member of the western North Atlantic species *Argopecten irradians* (Lamarck, 1819). This species determination is based in part on the morphological differentia among species of *Argopecten* described by Waller (1969). Specifically, the type specimen of *Pecten circularis* Sowerby can be identified with *Argopecten irradians* and can be distinguished from the accepted concept of “*Argopecten circularis*” for the following reasons:

(1) The disk flanks of the type are distinctly costate, whereas those of “*A. circularis*” are completely or nearly smooth.

(2) The posterior margins of the posterior auricles of the type are not deeply sigmoidal in shape, whereas those of "*A. circularis*" are.

(3) The auricular costae of the type are clearly expressed on all auricles, whereas in "*A. circularis*" these are generally weakly expressed, especially in the dorsal sectors of the auricles.

(4) The posterior half-diameter of the disk of the type is about equal to or is exceeded by the anterior half-diameter (see Waller, 1969), giving the shell a somewhat opisthocline appearance; in "*A. circularis*" the shell is less equilateral, with the posterior more extended than the anterior.

(5) The right valve of the type has only diffuse pigmentation, whereas the right valves in "*Argopecten circularis*" generally have boldly contrasting commarginal or oblique dark brownish or reddish pigment bars that contrast strongly with the light background of the remainder of the shell.

Rib number does not serve to distinguish "*Argopecten circularis*" from *A. irradians*. Both rib count and shell shape are important, however, for distinguishing subspecies of the latter (Waller, 1969), and the type specimen of *Pecten circularis* can be placed in the geographically central subspecies, *A. irradians concentricus* (Say, 1822).

This determination means that the specimen said to be Sowerby's type cannot have come from Guaymas, Mexico, the locality on the eastern side of the Gulf of California given by Sowerby (1835) with his original description. The habitat details given by Sowerby, "in sandy mud at a depth of seven fathoms," are consistent, however, with the level of detail accompanying many of the specimens in the Cuming Collection (see below), and Cuming's "careful attention to accurate documentation" was noted by Dance (1966:151) in his review of the history of this collection. This discrepancy then raises the question, if the specimen labeled as the type of *Pecten circularis* does not correspond to the data that accompany the specimen, is it in fact the type from the Cuming Collection described by Sowerby (1835)?

Sowerby I (1835, p. 110) introduced the name *Pecten circularis* with a brief Latin description without illustration:

Pect. testâ suborbiculari, tumidâ, subaequalvalvi, aequilateriali, fusco alboque variâ, auriculis magnis, subaequalibus; costis radiantibus octodecim interstitiis latioribus, arcuatim striatis; valvâ alterâ sulcis profundioribus: long. 1.5, lat. 0.8, alt. 1.4 poll.

Translation: Pecten shell suborbicular, inflated, subequivalved, equilateral, variegated dark whitish, with large, subequal auricles; 18 radiating ribs with wider interspaces having arcuate striae; other valve with deeper sulcus.

The occasion for the description was an evening meeting of the Zoological Society of London. As was typical of the meetings in those days, members brought specimens for

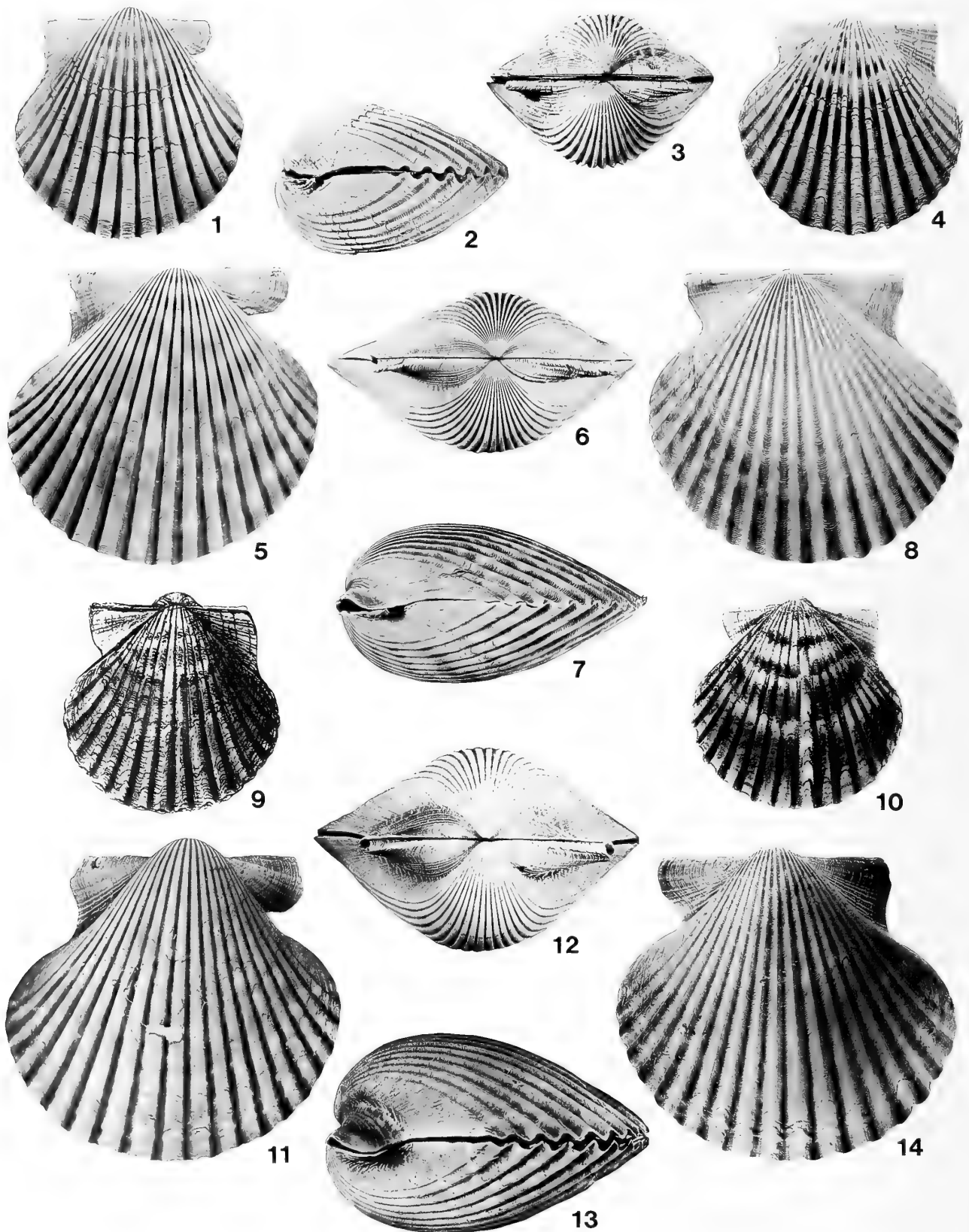
exhibit. In this case, the specimens brought to the meeting by Sowerby were from the collection of Hugh Cuming, a collector who entrusted his shells to others for description (Dance, 1966). The description itself is so generalized that it does not definitely establish that the specimen now marked as the type was the shell that Sowerby described. There is, however, nothing in the description that contradicts this possibility. The type specimen (left valve) has 18 ribs, as described, and the dimensions of the type correspond reasonably well to Sowerby's coarse measurements. The measurement term "poll." used by Sowerby refers to the pollex, a Latin word meaning "thumb" and used for the inch. If a similar coarse measurement unit, the modern inch rounded to the nearest tenth, is used, the dimensions of the specimen that is labeled as the holotype are length 1.5 inches, convexity of paired valves 1.0 inch, and height 1.5 inches. The apparent discrepancy between this measurement of convexity and that of Sowerby (0.8 poll.) may be the result of different measurement techniques.

Sowerby I (1835) provided no illustration, but he entrusted the task of illustrating specimens that he had described to his son, G. B. Sowerby II (Dance, 1966). Sowerby II (1842:51) repeated his father's description of *Pecten circularis* and provided the first illustration (his pl. 12, fig. 23, reproduced herein as Figure 9). It is important to note that Sowerby II added a comparison: "This species is not so rounded as *P. Nucleus*, and the auricles are larger and less obtuse." He also changed the locality for the species, giving "California and St. Vincent's," the latter referring to an island in the Antilles (and erroneous for both "*Argopecten circularis*" and *Argopecten irradians* as understood today). *Argopecten nucleus* (Born, 1778) is a Caribbean species which, like *A. irradians*, has costate disk flanks (Waller, 1969).

The small colored illustration of the left valve of the shell of *Pecten circularis* provided by Sowerby II (Figure 9) is informative, because it corresponds to the British Museum type in two features that would not be expected to occur in "*Argopecten circularis*" as that name is currently applied. First, the posterior margins of the posterior auricles are not deeply sigmoidal in shape; secondly, at least the posterior auricle is shown as having well-developed costae over its entire surface. Furthermore, the color is distinctly grayish, not reddish or yellowish as in "*Argopecten circularis*" as now understood. Lastly, the pigment pattern shown in the illustration roughly corresponds to that of the specimen labeled as the type. The most distinctive feature of this pattern in Sowerby's figure is a single dark ray on the left anterior auricle. This is also present on the type specimen.

Sowerby II provided a larger and more accurate figure for the eighth volume of the *Conchologia Iconica* published by Reeve (1852-1853:pl. 31, fig. 137), and Reeve gave a new description:

"Shell globose, very ventricose, equilateral, inequivalve valves, right the more convex, rayed with eighteen smooth



strong ribs, of which the interstices are excavated; ash-white, stained and variegated with greyish-black; ears equal."

Reeve modified the locality, "California (in sandy mud at seven fathoms); Cuming," and did not mention Guaymas, Mexico. The larger, more accurate illustration (Figure 10 herein) leaves little doubt that the specimen illustrated is the specimen labeled "holotype," based on the details of color pattern and growth check-marks on the shell surface.

The probability that Sowerby I (1835) had before him an Atlantic shell and not an eastern Pacific one helps to explain why he distinguished *Pecten tumidus*, said to be from Santa Elena [Ecuador], from *Pecten circularis*. The former name, a twice preoccupied junior homonym (see Grau, 1959) that was subsequently renamed *Pecten ventricosus* by Sowerby II (1842), is universally accepted as a synonym of *Pecten circularis* as that name is now applied. Sowerby II (1842) also did not include a comparison of *Pecten ventricosus* in his discussion of *Pecten circularis*.

The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985, Article 74b), cautions against inferring the existence of a holotype when it cannot be determined that a species name was established on a single specimen and when a holotype was not originally designated. In this case, however, it seems likely that the specimen bearing the number BMNH 1950.11.14.18-19 and illustrated herein (Figures 1-4) was indeed the only specimen available to Sowerby I for his original description of *Pecten circularis* and is therefore the holotype.

THE TYPES OF *ARGOPECTEN VENTRICOSUS*

Because the type of *Pecten circularis* Sowerby I (1835) was incorrectly named a new species by Sowerby and is in fact a specimen of *Argopecten irradians concentricus* (Say, 1822), Sowerby's name is a junior subjective synonym of the latter. The next available name in the synonymy list (Grau, 1959: 97) of *Pecten circularis* is *Pecten ventricosus* Sowerby II, 1842, a name that was introduced to replace the junior homonym, *Pecten tumidus* Sowerby I, 1835.

The locality of *Pecten tumidus* given by Sowerby I (1835: 110) is "Sanctam Elenam et ad Salango, Columbiae Occidentalis", referring to Santa Elena and Salango, both on the coast of Ecuador. Sowerby II (1842:52) repeated the

Santa Elena locality and added "and young specimens brought from Calapan, Philippines, by Mr. Cuming." The statement that the species occurs in the Philippines, which was repeated by Reeve (1852, Species 31), is erroneous.

Six specimens labeled *Pecten ventricosus* are present in the type collection of The Natural History Museum, London, and one of these specimens must be designated a lectotype if the name is to be fixed firmly. All of these type specimens consist of paired valves, and all conform to the established concept of Eastern Pacific "*Argopecten circularis*". Three of the specimens are associated with an old label, possibly in the hand of Sowerby II, which gives the locality as "St. Elena, Philippines"; the remaining three are associated with a similar old label that indicates the locality as "Philippine Is." The locality "Philippines" is clearly erroneous. The three specimens in the first lot (BMNH 1994116-1994118) are all brightly colored (orange, reddish, or lavender) and conform to the present-day concept of "*Argopecten circularis*," *sensu stricto*, rather than to the northern subspecies *Argopecten "circularis" aequisulcatus* (Carpenter, 1864) (see Waller, 1969). The three specimens in the second lot (BMNH 1994119-1994121), on the other hand, are mottled with very dark brown or maroon pigment and resemble specimens from more northerly localities, particularly those from La Paz, Mexico, but still within the range of variation of *A. "circularis*," *s.s.*. All six specimens are greater than 2 inches in length and thus exceed the value of "long. 1.75 poll." given by Sowerby I (1835, p. 110) in his original description of *Pecten tumidus*.

Sowerby II (1842:pl. 12, figs. 18, 19, 26) illustrated three specimens of *Pecten ventricosus*, only one of which (his pl. 12, fig. 18, BMNH 1994117) is possibly but not definitely among the specimens in the type collection on the basis of its bright orange color and color pattern. (The figure shows a posterior view, but the commissure of the posterior auricles is curiously reversed with respect to actual pectinid morphology.) The new and improved illustrations that Sowerby II prepared for Reeve (1852-1853: figs. 31a, 31b) represent two additional specimens, both of which are probably represented by specimens in the type collection. Fig. 31a corresponds exactly in size, dark brown mottling separated by pinkish to white areas, and the approximate pattern of these colors to one of the specimens in the second lot of three specimens referred to above

←

Explanation of Figures 1 to 14

Figures 1-4. *Argopecten irradians concentricus* (Say, 1822). Lectotype of *Pecten circularis* Sowerby I, 1835, BMNH 1950.11.14.18-19, from Guaymas, Mexico [erroneous], length 39.5 mm, right, anterior, dorsal, and left views. Figures 5-8. *Argopecten ventricosus* (G. B. Sowerby II, 1842), USNM 714198, from Guaymas, Mexico, length 53.8 mm, right, dorsal, anterior, and left views. Figures 9 and 10. Drawings of the left side of the type specimen

of *Pecten circularis* by Sowerby II (1842, Fig. 23) and Reeve (1853, Fig. 137), enlarged to match size of the actual type specimen shown in Figure 4. Figures 11-14. *Argopecten ventricosus*. Lectotype, BMNH 1994116, probably from Santa Elena, Ecuador, length 58.7 mm, right, dorsal, anterior, and left views. All specimens have been lightly coated with ammonium chloride to emphasize surface relief.

(BMNH 1994119, Figures 12–15 herein). Fig. 31b corresponds exactly in size and bright lavender hue to one of the specimens in the first lot (BMNH 1994116, Figures 12–15 herein). The second specimen (Reeve's fig. 31b) is selected herein as the lectotype, because it is the specimen with the color pattern that corresponds most closely to specimens known from Ecuador.

Selection of the lavender specimen as the lectotype (fig. 32b in Reeve, 1852–1853) rather than the dark brown-mottled specimen represented by Reeve's fig. 32a also avoids another potential problem. There is still no universal agreement on whether a northern geographic subspecies, *Argopecten* "circularis" *aequisulcatus* (Carpenter, 1864), should be recognized, and, if it is recognized, what its southern limit should be. As reviewed by Grau (1959: 101), the concept of a northern subspecies was originally based on populations in bays along the California coast from Santa Barbara southward. Grau himself continued to recognize the subspecies while acknowledging that it is only weakly differentiated from *A. "circularis circularis."* Others have considered it unnecessary to use a subspecies name because of the high degree of morphological intergradation (Waller, 1969; Bernard, 1983), while still others (McLean, 1978; Haderlie & Abbott, 1980) have considered the northern form to be a full species. *Argopecten aequisulcatus*. There has also been lack of agreement on the southern limit of the northern form. Grau (1959) gave the southern limit as Bahía San Quentín, northwestern Baja California, Mexico. Others, however, have considered the southern limit to be Cabo San Lucas (Dall, 1921; Fitch, 1953) or La Paz, Mexico (Keen, 1971), near the southern end of the Baja California peninsula. The southern form, *A. "circularis," sensu stricto*, extends from Isla Cedros, Mexico, and the Gulf of California southward to Paita, Peru, and westward to the Galapagos Islands (Grau, 1959). In order to avoid the issue of whether northern populations can be distinguished at the level of subspecies or species, a lectotype of *Argopecten ventricosus* preferably should be designated from a population where all specimens are clearly of the southern form. The logical choice would be a specimen from well south of Baja California. The lectotype chosen here, which is presumably from the Santa Elena, Ecuador, meets this requirement.

DISCUSSION AND CONCLUSION

It is unfortunate that the imperfection of past taxonomic work now requires that the name of a well-known species of commercial importance be set aside. The alternative would be to attempt to conserve the existing concept of *Argopecten circularis* by means of the plenary power provided by the International Code of Zoological Nomenclature. This has been used, in the interest of nomenclatural stability, to conserve names that are in universal use, a particularly desirable action in the case of the names of commercially or medically important species that are referred to frequently in the literature and where the res-

urrection of a junior name serves no useful biological purpose. In the case of a misidentified type specimen, Recommendation 75E, *International Code of Zoological Nomenclature* (International Commission on Zoological Nomenclature, 1985) states, "to resolve a complex zoological problem, a zoologist should refer the case to the Commission which may, by the use of the plenary power, set aside the existing type material and designate a neotype."

In the present case, however, the name *Pecten circularis* has already begun to be replaced by the name *Argopecten ventricosus* in papers dealing with fisheries and aquaculture (e.g., Villalaz, 1993, 1994; Villalaz & Gomez, 1994). The long-term benefit of nomenclatural stability would seem to be better served in this case by recognizing that the clearly identifiable holotype of *Pecten circularis* is actually a specimen of the Western Atlantic bay scallop, *Argopecten irradians*, and that the name *P. circularis* has been incorrectly applied to the Eastern Pacific species. The next available name for the Eastern Pacific species, *Pecten ventricosus*, is represented by a type series, one member of which has been designated here as the lectotype. This name in its modern form, *Argopecten ventricosus* (G. B. Sowerby II, 1842), should replace the name *Pecten circularis* in future studies.

ACKNOWLEDGMENTS

Encouragement to resolve this nomenclatural problem has come from P. L. Haaker of the California Department of Fish and Game, E. F. Felix-Pico, Centro Interdisciplinario de Ciencias Marinas, La Paz, Mexico, J. Villalaz R., Panama City, Panama, and Eugene V. Coan, California Academy of Sciences, San Francisco. I thank Ms. Kathie Way, Department of Zoology, The Natural History Museum, London, for the loan of specimens and for technical advice. Dr. Alan Kabat and Ms. Barbara Bedette of the National Museum of Natural History read the manuscript and gave suggestions for its improvement. Examination of specimens in London was made possible by a grant from the Research Opportunities Fund of the Smithsonian Institution.

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Reproductive Anatomy of *Vespericola shasta* (Berry, 1921) (Gastropoda: Pulmonata: Polygyridae), and Descriptions of Two New Species of *Vespericola* from Northern California

by

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Abstract. The reproductive anatomy of *Vespericola shasta* (Berry, 1921) is described. Two new species, *Vespericola rothi* and *Vespericola scotti*, are described and compared to *V. shasta* and to other *Vespericola* species with somewhat similar anatomies.

INTRODUCTION

Roth & Miller (1993) presented the first of a series of studies on the systematics of the West American polygyrid land snail genus *Vespericola* Pilsbry, 1939. Here we present the results of an investigation of the anatomy of topotypes of *Vespericola shasta* (Berry, 1921) and of the identity of four other vicinal populations.

Vespericola shasta was described by S. Stillman Berry on the basis of shell characters only. The type locality was given as La Moine, Shasta County, California. *Vespericola* populations from nearby localities (Flume Creek and 22 km from Sacramento River bridge on road from Volmer to McCloud River bridge), whose shells resembled those of *V. shasta*, were collected several years ago by one of us (W.B.M.) and provisionally catalogued as *V. shasta*. Upon examination of their anatomies, however, it was obvious that we had collected two very different species.

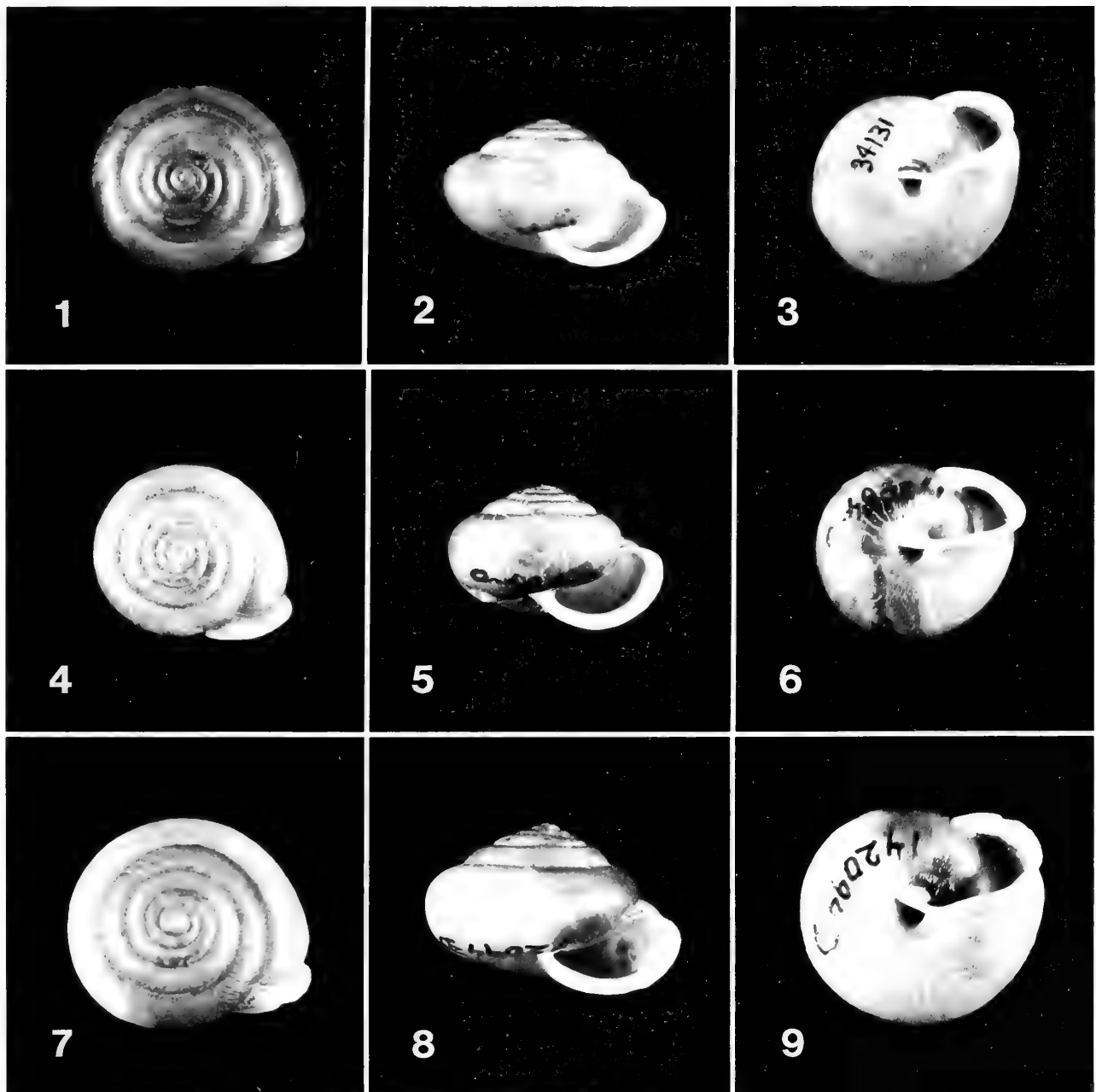
In order to determine which one, if either, was the real *Vespericola shasta*, it was necessary to obtain topotype specimens and examine their anatomies. One of us (W.B.M.) collected presumed topotypes from La Moine on 13 April 1994. There are two creeks at La Moine, Slate Creek and Little Slate Creek, which empty separately into the Sacramento River within 300 m of each other, and both had *Vespericola* populations. The locality at Little Slate Creek at La Moine most closely resembled the description of the type locality given by Berry; additionally, the shells of its *Vespericola* population were more similar to the holotype and paratypes than those from Slate Creek. Accordingly,

specimens from Little Slate Creek at La Moine were regarded as topotypes.

The specimens from Slate Creek and Flume Creek had anatomies similar to that of *Vespericola shasta* topotypes and are therefore considered to be *V. shasta*. This extends the range of the species by about 15 km to the north of La Moine. To determine if the range extended westward, specimens from a population of *Vespericola* from the Coffee Creek drainage, tributary to the Trinity River, about 35 km to the west of La Moine, were also dissected and examined. Their anatomies showed that they were a new species, described below as *Vespericola scotti*. Specimens from 22 km from the Sacramento River bridge on the road from Volmer to McCloud River bridge, roughly 15 km to the east of La Moine, collected and dissected in 1969, were also a new species. Fresh specimens from that locality could not be collected, however, because of road conditions, but specimens from a nearby population, with similar anatomies, were obtained and examined and are described below as *Vespericola rothi*.

MATERIALS AND METHODS

Shell height and diameter are vernier caliper measurements and exclude the expanded lip of mature shells. Whorls were counted by the method of Pilsbry (1939:xi, fig. B). The density of periostracal setae was estimated by counting the number of setae per square millimeter on the shoulder of the body whorl, 0.25 whorl behind the aperture of adult specimens, at 40× magnification under a dissecting mi-



Explanation of Figures 1 to 9

Figures 1–3. *Vespericola shasta* (Berry). Holotype, SBMNH 34131, California: Shasta County: La Moine, A. G. Smith coll., August 1921. Top, apertural, and basal views. Diameter 13.3 mm. Figures 4–6. *Vespericola scotti* Cordero & Miller, sp. nov. Holotype, SBMNH 142559, California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994. Top, apertural, and basal views. Diameter 12.8 mm. Figures 7–9. *Vespericola rothi* Cordero & Miller, sp. nov. Holotype, SBMNH 142560, California: Shasta County: along banks of Ellery Creek, near its confluence with Lake Shasta, under logs in briars, W. B. Miller coll., 27 May 1994. Top, apertural, and basal views. Diameter 16.4 mm. (This shell, selected as holotype, was originally numbered 142094–D; photograph taken prior to number change.)

crosscope with an ocular reticle. Three counts were taken per specimen, and the mean (to the nearest integer) recorded.

Specimens for dissection were prepared by the method of Miller (1967). Snails were first drowned in water to ensure expansion and relaxation, then heated to a temperature of 60°C, at which time the bodies could be pulled easily from the shells and dissected. After the body cavity was opened, the position and maturity of the reproductive system were observed; then the whole reproductive system was removed, attached to a small patch of body wall around the external genital orifice. The penis was slit longitudinally to expose the verge of at least one specimen from each locality.

Whole mounts of genitalia were prepared by the method of Miller (1967): stained with hematoxylin and eosin, dehydrated and cleared in successive baths of ethanol and toluene, and mounted on slides with Permount mounting medium. Organ measurements were taken from dissected specimens. Anatomical drawings were made by projecting the image of the whole mount on paper with an overhead projector.

Shell growth in Polygyridae is determinate and ends with, first, a constriction of the body whorl and then a turning outward and thickening of the lip. Reproductive maturity normally seems to follow a short time after the lip turns, but the presence of a turned lip does not guarantee a reproductively mature specimen. Therefore, at least a portion of each sample was kept alive in a terrarium for a period of weeks or months to ensure full development of the genital structures. Terraria consisted of redwood boxes with screened tops. A 3–6 cm layer of soil and leafmold from the collecting locality was added. Specimens were fed lettuce. There is no indication that growth of *Vespericola* in terraria under these conditions is in any way abnormal.

The following abbreviations are used: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; FMNH, Field Museum of Natural History; SBMNH, Santa Barbara Museum of Natural History.

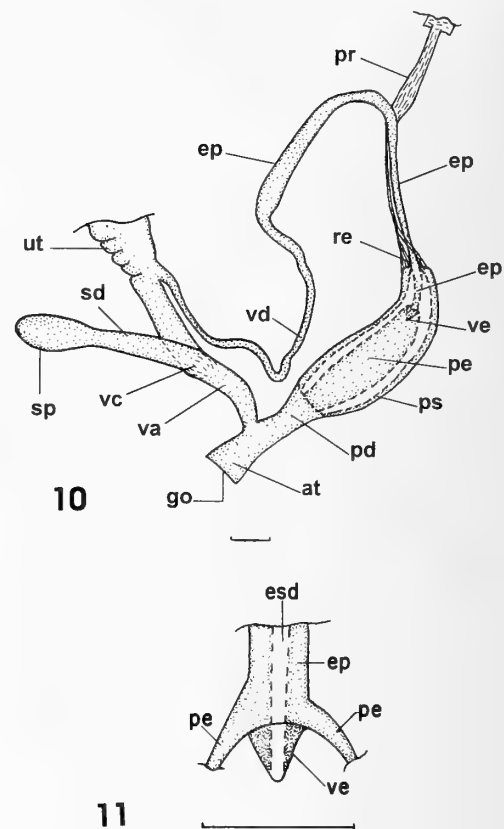
SYSTEMATICS

Vespericola shasta (Berry, 1921)

(Figures 1–3, 10–11)

Polygyra columbiana shasta Berry, 1921:37, pl. 2, figs. 6, 7.
Vespericola shasta (Berry), Pilsbry, 1939:903–904, figs. 518d, 518d', 518f, 518g.

Diagnosis: A small *Vespericola* with depressed-helicoid to conical, moderately umbilicate shell, usually with a parietal lamella, those from the type locality mostly smooth, glossy, and without periostracal setae; a few shells with about one or two setae/mm². Shells from conspecific vicinal populations with four to seven periostracal setae/mm². Penis elongate-conical, entirely enclosed by the penial



Explanation of Figures 10 and 11

Figures 10, 11. *Vespericola shasta* (Berry). Drawings made from projections of stained whole mounts of topotypes. Figure 10. Anterior portion of reproductive system, SBMNH 142066, California: Shasta County: La Moine: Little Slate Creek: in leaf-mold-covered rocks above edge of creek on right bank, W. B. Miller coll., 13 April 1994. Figure 11. Part of epiphallus and apical end of penis opened to show verge, SBMNH 142066, collection data same as above. Abbreviations for anatomical figures: at, atrium; ep, epiphallus; esd, epiphallallic seminal duct; go, genital orifice; lu, lumen of epiphallallic seminal duct; ov, oviduct; pe, penis; pd, peduncle; pr, penial retractor; ps, penial sheath; re, retentor; sd, spermathecal duct; sp, spermatheca; ut, uterus; va, vagina; vc, vaginal collar; vd, vas deferens; ve, verge. Scale lines in anatomical figures = 1 mm.

sheath, which also encloses part of the proximal epiphallus; verge 0.2 to 0.3 mm long, conical, with seminal duct opening at the blunt tip.

Description of holotype: Shell medium-sized for the genus (diameter 13.3 mm) broadly conical, narrowly umbilicate, with 5¾ whorls. Spire weakly convex; whorls rounded, suture strongly impressed. Embryonic whorls indistinguishable from later whorls. Sculpture consisting of numerous and fairly strong rugae, much weaker on the base; surface polished and lustrous, without periostracal

setae. Periphery smoothly rounded. Base tumid, lustrous. Umbilicus contained about 12 times in diameter. Body whorl deflected downward, slightly constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile. Lip turned outward and expanded, somewhat reflected at base. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly dilated, covering one-third of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: Nine topotypes from Little Slate Creek, La Moine, California, were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, completely enclosed in thin sheath adnate to base (Figure 10). Short, peduncular portion of about 0.6 mm present between base of the sheath and the junction with the atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing minuscule conical pointed verge varying from 0.2 to 0.3 mm long and 0.2 to 0.3 mm wide at its base. Seminal duct opening into penial chamber at cleft tip of verge (Figure 11).

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to the summit of the penial sheath, from which other retentor fibers form connections with parts of the epiphallus and vas deferens.

In the nine topotypes, sheath length varying from 4.2 to 5.7 mm, with mean of 4.6 mm. On average, sheath extending 1.1 mm beyond apical end of penis.

Spermathecal duct narrow, tightly appressed to free oviduct (which is smaller in diameter and branches from it), about 2.6 mm long, about 0.6 mm in diameter at junction with oviduct, tapering gradually to 0.4 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 1.9 mm long and 1.3 mm in diameter, with bluntly pointed tip.

Slight swelling on vagina present at junction of spermathecal duct and oviduct in most dissected topotypes.

Type material: Holotype: SBMNH 34131. Paratypes: SBMNH 34132. Paratypes also deposited by the author in the collections of the CAS, ANSP, and Leland Stanford Junior University, as well as the private collection of Allyn G. Smith, subsequently also deposited in the CAS.

Distribution: Shasta County, California, along Flume Creek near its confluence with the Sacramento River and at La Moine, along Slate Creek and Little Slate Creek near their confluences with the Sacramento River.

Remarks: The type locality of *Vespericola shasta* is La Moine, with no more exact location specified. At La Moine, two creeks, Slate Creek and Little Slate Creek, empty

directly into the Sacramento River within 300 m of each other. Slate Creek is the larger creek, with steep banks and swiftly flowing water, offering very little shelter at the water's edge. Only three live specimens were collected along Slate Creek, while about 20 were collected at Little Slate Creek. Allyn G. Smith, who collected the type lot of 25 specimens in August 1921 found them "almost in the water under sticks and stones" (Berry, 1921). Furthermore, Berry emphasized that the features which served to set this species quite distinctly apart were its warm brown color, smooth, polished surface, lack of any sort of persistent periostracal fringes, and narrow, though permeable umbilicus. The specimens from Little Slate Creek reflect all of these characters, while those from Slate Creek had persistent periostracal setae, about 4–7/mm². Although this character is considered insufficient to suggest reproductive isolation and speciation, it does serve to narrow down the type locality to Little Slate Creek. Accordingly, specimens from Little Slate Creek are considered topotypes. The two specimens from Slate Creek had anatomies which showed no significant differences from those from Little Slate Creek and are therefore considered to be conspecific.

Two specimens from Flume Creek, which empties into the Sacramento River about 15 km to the north, also had persistent periostracal setae about 1–3/mm². Other shell characters, as well as anatomical characters, were similar to those of Little Slate Creek and therefore this population is considered to be conspecific, thereby extending the range of the species northward to Flume Creek.

Anatomically, *Vespericola shasta* is distinguished from other species by its penial sheath, which not only encloses the entire penis, but also a portion of the proximal epiphallus, and by its minuscule, conical, pointed verge.

Vespericola scotti Cordero & Miller, sp. nov.

(Figures 4–6, 12–13)

Diagnosis: A small to medium-sized *Vespericola* with depressed-helicoid to broadly conical, narrowly umbilicate shell, 5½ to 5¾ whorls, 3–12 periostracal setae/mm², usually with a parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.3; verge minuscule, consisting only of a rim papilla at the tip of the epiphallus, about 0.1 mm high, barely protruding into the penial chamber.

Description of shell: Shell small to medium-sized for the genus (diameter 11.2 to 13.1 mm) depressed-helicoid to broadly conical, narrowly umbilicate, with 5½ to 5¾ whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae. Periostracum bearing slender setae, 3–12/mm² on shoulder of body whorl. Surface between setae densely, smoothly granulose on spire and body whorl and collabially wrinkled. Periphery simply rounded. Base

tumid, smooth. Umbilicus contained about 15–21 times in diameter. Body whorl deflected downward, slightly constricted behind lip. Aperture broadly auriculate; peristome shallowly concave in profile. Lip turned outward and expanded, somewhat reflected at base. Parietal lamella usually present. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering one-half to three-fourths of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: The holotype and 18 paratypes were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, anterior, basal part enclosed in thin sheath adnate to base; protruding part stout and markedly curved. Short, peduncular portion of about 0.9 mm present between base of sheath and junction with atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing minuscule verge consisting of a circular, protruding papilla at tip of seminal duct, insufficiently long to converge into a pointed tip, 0.1 mm long and 0.3 mm wide at its base, the perimeter of the seminal duct (Figure 13).

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to summit of penial sheath, from which other retentor fibers form connections with parts of epiphallus and vas deferens.

Sheathed part of penis in the holotype about 5.2 mm in length; protruding part about 4.6 mm long. In the 18 paratypes, sheath length varying from 2.5 to 5.8 mm, with mean of 4.6 mm; protruding part varying from 4.1 to 7.8 mm in length, with mean of 6.0 mm. Mean ratio of protruding length to sheathed length about 1.3.

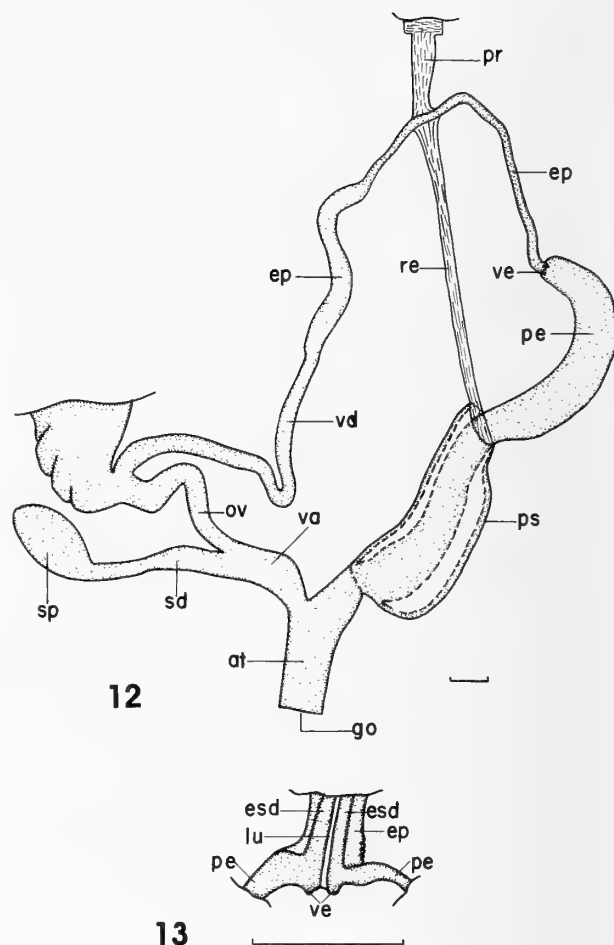
Spermathecal duct moderately swollen at base where it joins oviduct, tightly appressed to free oviduct, about 2.6 mm long, tapering from about 0.7 mm diameter at junction with oviduct to 0.3 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 2.6 mm long and 1.3 mm in diameter, with bluntly pointed tip.

Type material: Holotype: SBMNH 142559 (shell and stained whole mount of reproductive system), California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994.

Paratypes: SBMNH 142084 (12 shells and stained whole mounts of reproductive system), from same locality as holotype. Additional paratypes deposited in ANSP and FMNH.

Distribution: This species is currently known only from the type locality.



Explanation of Figures 12 and 13

Figures 12, 13. *Vespericola scotti* Cordero & Miller, sp. nov. Drawings made from projections of stained whole mounts of paratypes. Figure 12. Anterior portion of reproductive system, SBMNH 142084, California: Trinity County: along Benson Gulch, ca. 500 m from its confluence with Coffee Creek, at edge of stream under bark and logs, W. B. Miller coll., 23 May 1994. Figure 13. Longitudinal section of junction of epiphallus with penis, showing verge papilla, SBMNH 142084, collection data same as above. Abbreviations for anatomical figures as for Figures 10, 11. Scale lines in anatomical figures = 1 mm.

Remarks: By shell characters, *Vespericola scotti* is difficult to separate from populations of *V. shasta* that have sparse periostracal setae such as those from Slate Creek and Flume Creek.

Anatomically, however, *Vespericola scotti* differs from all other known species of *Vespericola* by its verge which consists only of a minuscule rim papilla at the end of the epiphallus, about 0.1 mm in height, barely protruding into the penial chamber, insufficiently long to converge into a conical tip. Its recurved, stout and long protruding penis also separates it from other species.

Vespericola scotti has been found only in a very limited

habitat, along the edge of a small running stream descending steeply in Benson Gulch about 500 m from its confluence with Coffee Creek. The majority of living adults were found under large pieces of alder bark that were kept partially wet by the stream water. The dominant trees in the gulch are Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), and incense cedar (*Calocedrus decurrens*), with an understory of big leaf maple (*Acer macrophyllum*), red alder (*Alnus oregona*), and Pacific dogwood (*Cornus nutallii*).

Etymology: This species is named for Paul Scott of the SBMNH, who made it possible for us to collaborate and assisted us greatly in the preparation of this article.

Vespericola rothi Cordero & Miller, sp. nov.

(Figures 7–9, 14–15)

Diagnosis: A medium-sized to large *Vespericola* with depressed-helicoid to broadly conical, widely umbilicate shell, the umbilicus nearly half-covered by the columnella, $5\frac{3}{4}$ to 6 whorls, 2–7 periostracal setae/mm², without parietal lamella. Penis elongate-conical, ratio of protruding part to sheathed part approximately 1.0; verge 0.5 mm long, conical, ending in a blunt tip. Conspicuous swelling on vagina at junction with spermathecal duct and oviduct.

Description of shell: Shell medium-sized to large for genus (14.2 to 16.9 mm in diameter) depressed-helicoid to broadly conical, widely umbilicate, with $5\frac{3}{4}$ to 6 whorls. Spire straight-sided or weakly convex; whorls rounded, suture moderately to strongly impressed. Embryonic whorls 1.5. Early teleoconch whorls with inconspicuous, crowded, retractive growth rugae. Periostracum bearing slender, sparse setae, 2–7/mm² on shoulder of body whorl. Surface between growth wrinkles microscopically granulate. Periphery simply rounded. Base tumid, smooth. Umbilicus contained about 13–16 times in diameter, with persistent periostracal setae and papillae. Body whorl deflected downward, moderately constricted behind lip. Aperture roundly lunate; peristome shallowly concave in profile. Lip narrowly reflected, somewhat thickened at base. Parietal lamella absent. Inner part of basal lip gently angled forward, weakly to moderately dilated, covering one-fourth to one-half of the umbilicus. Periostracum warm brown; lip pale tan to white.

Description of soft anatomy: The holotype and three paratypes were dissected.

Color of living animals tan, darker and grayer on the body-stalk. Mantle over lung clear buff, 30% to 50% maculated with black.

Penis elongate-conical, anterior, basal part enclosed in thin sheath adnate to base. Short, peduncular portion of about 1.1 mm present between base of sheath and junction with atrium. Interior of penial chamber bearing papillose pilasters in diverging V-pattern. Apex of penis containing short, conical pointed verge 0.5 mm long and 0.5 mm wide

at its base. Seminal duct opening into penial chamber at cleft tip of verge.

Penial retractor muscle inserted on epiphallus. Retentor extending from penial retractor muscle insertion to summit of penial sheath, from which other retentor fibers form connections with parts of epiphallus and vas deferens.

Sheathed part of penis in the holotype about 7.0 mm in length; protruding part about 5.5 mm in length. In the three paratypes, sheath varying from 5.1 to 7.0 mm in length, with mean of 5.9 mm, protruding part varying from 5.2 to 7.0 mm in length, with mean of 5.9 mm. Mean ratio of protruding length to sheathed length about 1.0.

Spermathecal duct moderately wide, tightly appressed to free oviduct (which is smaller in diameter and branches from it), about 4.6 mm long, gradually tapering from about 1.2 mm in diameter at junction with oviduct to 0.6 mm diameter constriction at base of spermatheca.

Spermatheca oblong-ovate in fully mature specimens, narrowly cylindrical in less mature individuals, about 5.9 mm long and 3.0 mm in diameter, with bluntly pointed tip.

Conspicuous swelling on vagina at junction of spermathecal duct and oviduct in all dissected types.

Type material: Holotype: SBMNH 142560 (shell and dissected anatomy), California: Shasta County: Ellery Creek about 200 m from its confluence with Lake Shasta, W. B. Miller and B. Roth coll. 27 May 1994.

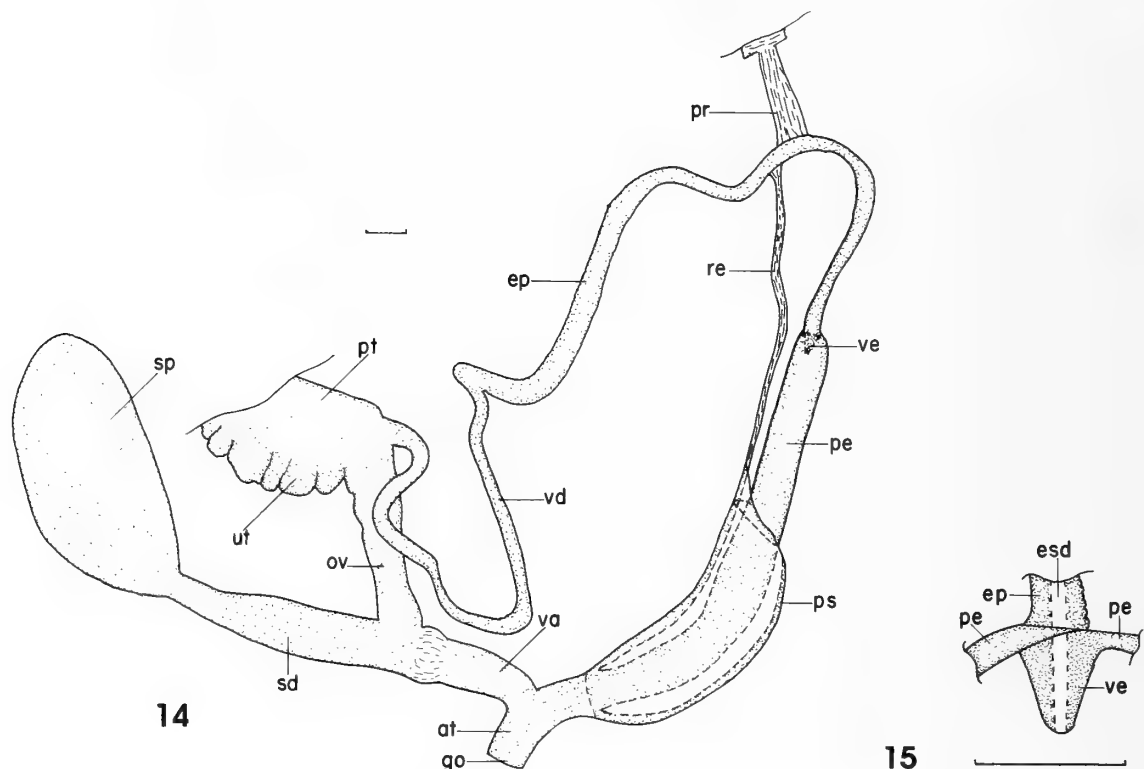
Paratypes: SBMNH 142094 (3 shells and stained whole mounts of reproductive system), from same locality as holotype.

Referred material: California: Shasta County: Along road from Volmer to McCloud River bridge at a ravine 22 km from Sacramento River bridge. SBMNH 75185 (20 shells and 2 stained whole mounts of reproductive system); W. B. and W. N. Miller coll., 15 August 1969.

Distribution: Shasta County, California, along lower end of Ellery Creek and along unnamed limestone ravine with running stream along old road from Volmer to McCloud River bridge about 22 km from Sacramento River bridge.

Remarks: The specimens listed above under Referred Material consisted of 18 living adults which were actively crawling along the wet edge of a small stream in an unnamed limestone ravine along the road. In shell size (11.3 to 14.7 mm in diameter) they are markedly smaller than the types from Ellery Creek; the umbilicus is relatively wide, contained 10–13 times in the diameter and similarly covered one-fourth to one-half by the inner lip; the shells are smooth and glossy, without periostracal setae. Anatomically, they are similar in all respects to the types except for being proportionally smaller.

The absence of periostracal setae in this population versus their sparse occurrence (2–7/mm²) in the type population mirrors the situation in *Vespericola shasta* for populations from the type locality, Little Slate Creek, versus



Explanation of Figures 14 and 15

Figures 14, 15. *Vespericola rothi* Cordero & Miller, sp. nov. Drawings made from projections of stained whole mounts. Figure 14. Anterior portion of reproductive system of holotype, SBMNH 142560, California: Shasta County: along banks of Ellery Creek, near its confluence with Lake Shasta, under logs in briars, W. B. Miller and B. Roth coll., 27 May 1994. Figure 15. Part of epiphallus and apical end of penis opened to show verge of paratype. SBMNH 142094, collection data same as above. Abbreviations for anatomical figures as for Figures 10, 11. Scale lines in anatomical figures = 1 mm.

those from Slate Creek and Flume Creek. Furthermore, instances of marked disparity in shell diameter between populations of the same species of *Vespericola* have been observed in *Vespericola marinensis* Roth & Miller, 1993, as well as in *Vespericola columbianus* (Lea, 1838), *Vespericola megasoma* (Pilsbry, 1928), and *Vespericola euthales* (Berry, 1939) (Roth & Miller, unpublished observations).

Accordingly, the specimens from this unnamed limestone ravine are considered to be conspecific with the Ellery Creek types.

Vespericola rothi exhibits anatomical characters similar to those of *Vespericola pressleyi* Roth, 1985, in that the penis is long, with a protruding part to sheathed part ratio of about 1.0, and the verge is short, conical, and about 0.6 mm long. In *V. pressleyi*, however, the entire penis is markedly thin, about 0.5 mm in diameter along its entire length almost to the base where it abruptly widens to a base diameter of 0.9 to 1.0 mm. In *V. rothi*, the penis is stout, cylindrical for its entire length, about 1.0 mm in diameter. Additionally, *V. pressleyi* consistently has a massive spermathecal duct, about 1.4 mm in diameter at its junction

with the oviduct and no enlarged vaginal collar; *V. rothi*, however, has a relatively thin spermathecal duct, 1.1 mm at its base, and a large vaginal collar is present in all specimens dissected.

Vespericola rothi differs from *Vespericola pressleyi* and other known species of *Vespericola* in shell characters by its wide umbilicus which is one-fourth to one-half covered by the reflected columellar lip; in *V. pressleyi*, the inner lip is not markedly dilated over umbilicus (Roth, 1985).

Vespericola rothi appears to be an obligate calcicole, living only at the water's edge in limestone ravines. *Vespericola pressleyi*, in contrast, has been found in large numbers in acidic humus under decaying fir logs near its type locality close to Big Bar Ranger Station, Trinity County, California.

The vegetation along lower Ellery Creek consisted primarily of willows with intertwining blackberry vines and stinging nettles so thick as to make the area almost impassable.

Etymology: The species is named for Dr. Barry Roth who

suggested and led the expedition to Ellery Creek in his continuing effort to study the speciation and distribution patterns of *Vespericola*.

ACKNOWLEDGMENTS

We are grateful to the University of California, Santa Barbara Summer Academic Research Internship (SARI) and to Dorothy Nagaran for her effort in making it possible for one of us (A.M.C.) to work at the Santa Barbara Museum of Natural History. We also wish to thank Eric Hochberg and Paul Scott who provided us with facilities, equipment, and material of the museum as well as considerable assistance in the preparation of the manuscript. We also wish to thank Henry Chaney for reviewing the manuscript. Barry Roth assisted us in lending specimens of *Vespericola pressleyi* for comparative purposes and in encouraging us to prepare this manuscript.

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Late Pleistocene Mollusks from the Dolomite Site, Owens Lake Playa, California

by

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Abstract. A late Pleistocene mollusk assemblage from a wave-cut terrace from the Dolomite site, Owens Lake, California, was analyzed. A radiocarbon date of $11,400 \pm 60$ yr B.P. was obtained on articulated *Anodonta californiensis* shells. Associated mollusks included *Sphaerium striatinum*, *Pisidium compressum*, *Valvata humeralis*, *V. utahensis*, *Helisoma newberryi*, and *Vorticifex effusa*. This information was compared to an undated mollusk record from Point Bartlett and provides evidence concerning the late Pleistocene environments at Owens Lake. Based on the mollusks identified, the Dolomite site contains an assemblage indicative of deeper-water conditions than that of the Point Bartlett site. Evidence from the Dolomite site indicates that the maximum surface elevation of Owens Lake during the latest Pleistocene was at least +1097 m MSL. During the waning stages of the last glaciation, wetter than present conditions existed, because a Utah juniper woodland existed in Owens Valley.

INTRODUCTION

Within the intermountain region of eastern California, the valley-floor playas are indicative of extensive Pleistocene pluvial lakes. During the late Wisconsin glacial stage (23,000–10,000 yr B.P.), glaciers covered the Sierra Nevada, a juniper woodland existed across the Mojave Desert, and the valley floors contained lakes. The wetter than present climates caused a system of pluvial lakes to expand in size and volume. Occasionally, some pluvial lakes reached levels where they overflowed their basins and established connections with the next downstream lake. The Owens River lake chain began at the headwaters of the Owens River in Long Valley (Figure 1).

This report analyzes a radiocarbon-dated mollusk accumulation from the Dolomite site at Owens Lake, and compares this assemblage to a published study of mollusks from the western shore of Owens Lake at Point Bartlett (Miller, 1989; Figure 1). These records allow a more comprehensive picture of the late Pleistocene environments in Owens Valley.

Owens Lake was the second lake in the Owens River lake chain system (Figure 1). Today, Owens Lake contains a watershed of 8500 km², but receives nearly all of its incoming waters from only the 16% of watershed that occurs on the eastern Sierra Nevada (Lee, 1912; Smith & Street-Perrott, 1983). However, today virtually all of Owens Lake's incoming waters are diverted to Los Angeles,

leaving only a playa (surface elevation = 1081 m). Prior to 1912, Owens Lake had a surface area of 290 km² and was as much as 10 m deep (Smith & Street-Perrott, 1983). In the past, the lake level rose to 1145 m, causing the lake to overflow into the basin of Searles Lake. The Owens River system eventually terminated at Lake Manly in Death Valley (Smith & Street-Perrott, 1983).

Site

Owens Lake is located in the south end of Owens Valley, Inyo County, California (Figure 1). The Dolomite site (31°50'N, 117°54'W; T. 16 S, R. 37 E, sec. 23, NW ¼) is located 4.5 km east-southeast of the Owens River inlet and 2 km southeast of the abandoned town of Dolomite, at +1097 m above MSL. The collection site is found in a wave-cut terrace having abundant *Anodonta californiensis* (Lea, 1852) shells weathering from a presumed lake bottom deposit (Figures 2, 3). Wave-cut terraces are common in the area.

MATERIALS AND METHODS

A 50 cm-deep excavation was made to remove the sandy overburden exposing many articulated *Anodonta* shells (Figure 3). Approximately 300 grams of *Anodonta* shell were recovered from approximately 4 liters that were dry-screened (1 mm mesh) on site. An additional 2.5 liters of

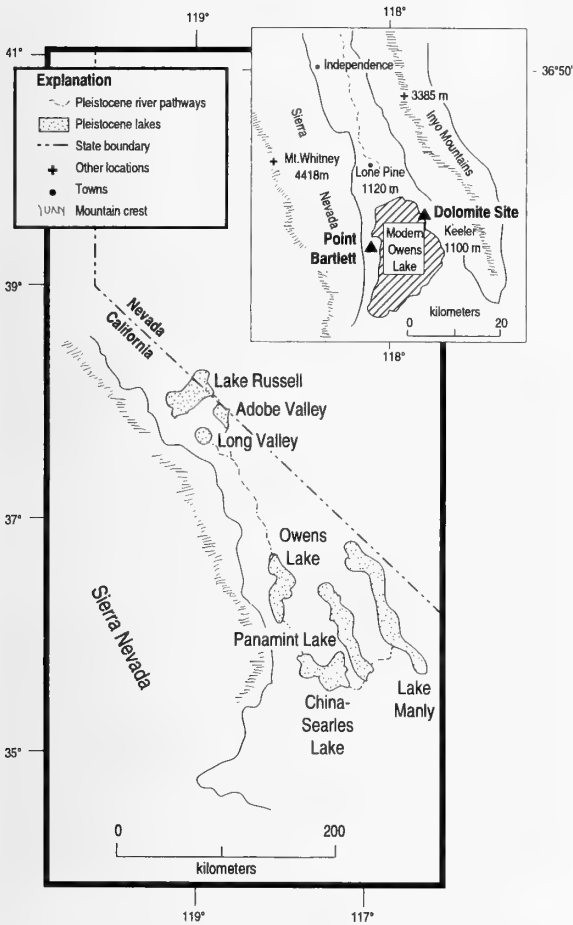


Figure 1

Map depicting the Pleistocene Owens River Lake chain at maximum highstand. Inset: Mollusk sites at modern Owens Lake (Map after Smith & Street-Perrott, 1983).

bulk material were recovered and brought to the Laboratory of Paleoecology, Northern Arizona University, for analysis. The bulk material was screen-washed through a pair of nested sieves (0.8 mm and 0.25 mm) for the recovery of smaller molluscan remains. The remains were sorted under a dissecting microscope (7 to 40×) and identified using published material (Burch, 1989; Herrington, 1962) and the reference mollusk collection at the Quaternary Studies Program, Laboratory of Paleontology. Molluscan nomenclature follows Burch (1989) and Herrington (1962). Representative specimens are deposited in the Northern Arizona University Quaternary Studies Program Mollusk collection under NAUQSP mollusk collection #7510–7516.

A radiocarbon date was obtained on recovered *Anodonta* shells. Whole shells were inspected under a dissecting microscope for visible carbonate contamination. Selected shells were handwashed until the nacre was fully exposed and treated with ultrasonic vibration to disarticulate the shell along the growth lines. The disarticulated shell was then

Table 1

Relative abundances of mollusks identified from Owens Lake. Point Bartlett material is based on Miller (1989). The relative abundance of mollusks is represented with the following numbers: 5 = >500 individuals/liter; 4 = 500 to 251 individuals/liter; 3 = 250 to 101 individuals/liter; 2 = 100 to 21 individuals/liter; 1 = < 20 individuals/liter. * Denotes variation due to depositional context.

Taxa	Point Bartlett	Dolomite
Pelecypoda		
<i>Sphaerium striatinum</i> (Say, 1829)	—	1
<i>Pisidium compressum</i> (Prime, 1852)	—	5
<i>Pisidium</i> sp.	1–2*	—
<i>Anodonta californiensis</i> (Lea, 1852)	—	1
Gastropoda		
? <i>Amnicola</i> sp.	1	—
<i>Valvata humeralis</i> (Pilsbry, 1908)	1–3*	2
<i>V. utahensis</i> (Call, 1884)	1–3*	4
<i>Helisoma</i> (<i>Carinifex</i>) <i>newberryi</i> (Lea, 1858)	2–5*	5
<i>Gyraulus parvus</i> (Say, 1817)	1	—
? <i>Planorbula</i> sp.	1	—
<i>Vorticifex</i> (<i>Parapholix</i>) <i>effusa</i> (Lea, 1856)	1–5*	2
<i>Physa</i> sp.	1	—
lymnaeid	1	—

treated with 3–5% HCl solution. This procedure yielded 100 grams of treated material that was dated by Beta Analytic (Miami, Florida).

RESULTS

Depositional Environment

Shoreline deformation has been recorded at Owens Lake (Carver, 1975). The area near the Dolomite site records a 4° inclination, while Point Bartlett records 3.6–15° inclination. Miller (1989) discussed the taphonomic importance of folded lake beds and winnowing of molluscan assemblages during erosion at Point Bartlett. Evidence for this type of effect has not been noted at the Dolomite site.

The sediments containing the Dolomite mollusks consist of silty sands. The sands contain mainly subangular to subrounded quartz sand grains probably derived from the Cretaceous granitic rock which predominates in the region. Larger, well-rounded pebbles (to 2 cm diameter) found in the sediments are mostly vesicular basalt, welded tuff, and obsidian. A radiocarbon date of 11,400 ± 60 yr B.P. (Beta-67673) was obtained on *Anodonta* shell. The dating of freshwater mollusks is problematic and should be taken as a general estimate of the true age. Although care was taken to remove macroscopic carbonate, submicroscopic carbonate contamination may have been present. Factors that might have affected the carbon-isotope composition of mollusk shells include the assimilation of dead or inactive carbon through ingestion and/or incorporation through



Figure 2

The Dolomite site in the wave-cut terrace. View is toward the east with the Inyo Mountains in the background.

groundwater discharge into the lake (Riggs, 1984). Another condition, the biological-isotope effect, exists where preferential fractionation of heavier carbon isotopes is assimilated during carbonate precipitation (Benson et al., 1990). These mechanisms could lead to a date that appears older than the true date.

Taxa and Taphonomy

Miller (1989) described an undated mollusk assemblage from Point Bartlett, Owens Lake (Figure 1; Table 1). Ten species of mollusks were identified from Point Bartlett, whereas the Dolomite site contained only seven taxa. Both sites contain *Helisoma* (*Carinifex*) *newberryi* (Lea, 1858) as the dominant taxon. The Point Bartlett site also contains larger *Helisoma newberryi* with a maximum diameter of 19.5 to 16 mm, depending on depositional context, while the Dolomite site records a maximum diameter of 17.5 mm with an average size of ca. 10 mm (Figure 4). *Vorticifex* (*Parapholix*) *effusa* (Lea, 1856) is recorded as the second most abundant taxa at the Point Bartlett site, but it is

uncommon at the Dolomite site. Point Bartlett records an average shell size of 11–8.5 mm, while the Dolomite site records 6.5 mm. These variations in shell size may be the result of an environmental effect. Larger size might be attributed to a higher water temperature and/or nutrient availability at specific sites. The shells recovered from the Dolomite site appear to be thicker than those from Point Bartlett. Possibly, this is related to the available calcium carbonate in the water.

Other species that were common at the two sites are the prosobranchs *Valvata humeralis* (Pilsbry, 1908) and *V. utahensis* (Call, 1884). The major species difference between the two sites is the presence of the gastropods *Gyraulus parvus* (Say, 1817), *Physa* sp., an unidentified lymnaeid, *?Amnicola* sp., and *?Planorbula* sp. found only at Point Bartlett, all of which were uncommon. Two species of pelecypods, *Anodonta californiensis* and *Sphaerium striatinum* (T. Say, 1829), were found only at the Dolomite site.

Observation of shell surface conditions at the Point Bartlett site shows that >5–90% of the shell material recovered



Figure 3

Silty sands and mollusks at the study site. Note the articulated *Anodonta californiensis* in the middle of the photo.

was blackened, possibly due to anaerobic conditions of the lake environment (Miller, 1989). The Dolomite site does not contain any blackened shells; however, many of the shells showed signs of predepositional wear. Surficial erosion of the shells can be observed, especially along the outer edges (Figure 4). Substantial reworking of the assemblage is unlikely because of the various sizes of shells represented (Figure 4).

Mollusk Ecology

The gastropod species identified from Owens Lake are associated with permanent to semipermanent lacustrine environments. Today, many of these species are restricted to the periphery of the Great Basin and northern California (Taylor, 1981). *Vorticifex effusa* is common in larger lakes, rivers, springs and spring-fed streams, and restricted to perennial, well-oxygenated water (Taylor, 1981; Burch, 1989). It was also common in the Pleistocene western pluvial system (Baily & Baily, 1952). *Helisoma newberryi* is found at present in the Sierra Nevada north of Lake

Tahoe in upland lakes and streams (Storer & Usinger, 1963), and was formerly found in the Owens River system (Taylor, 1981). This species was common to past pluvial lake environments, including lakes within the Owens River system (Baily & Baily, 1952; Taylor, 1985). Today, it is found in a habitat of larger lakes and slow rivers, and characteristically burrows into soft mud (Taylor, 1981). *Valvata humeralis* is at present widely distributed in the intermountain west and prefers the small perennial waters of lakes, ponds, and marshes (Taylor, 1981; Burch, 1989). It lives on mud bottoms and is common in dense aquatic vegetation (Taylor, 1981). *Valvata utahensis* is at present restricted to Utah and Idaho and inhabits large perennial water environments (Taylor, 1985; Burch, 1989).

Three pelecypod species have been identified at Owens Lake. *Anodonta californiensis* is a large clam and is confined to the drainages of the Pacific Ocean. Today, this species is recorded in Oregon, California (including the Owens River system), Utah, and Arizona (Bequaert & Miller, 1973; Taylor, 1981). *Anodonta* lives in large perennial waters and requires a specific host fish for glochidia (Be-

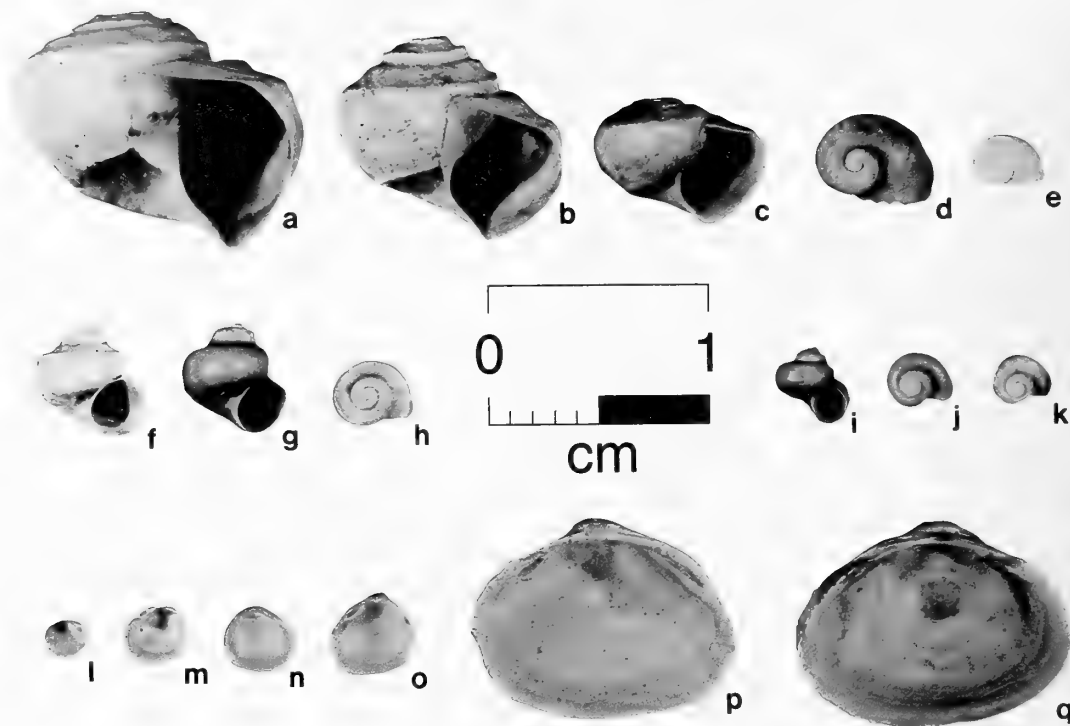


Figure 4

Recovered mollusks from the Dolomite site. *Helisoma newberryi* (NAUQSP 7515) a-c; *Vorticifex effusa* (NAUQSP 7510) d, e; *Valvata utahensis* (NAUQSP 7511) f-h; *V. humeralis* (NAUQSP 7513) i-k; *Pisidium compressum* (NAUQSP 7512) l-o; *Sphaerium striatinum* (NAUQSP 7514) p, q.

quaert & Miller, 1973; Taylor, 1981). *Sphaerium striatinum* occurs throughout North America and northern California (Herrington, 1962; Bequaert & Miller, 1973; Taylor, 1981). It is found in clean permanent waters, never in stagnant waters, at depths of several centimeters to 13.5 m and prefers sandy to gravelly substrates (Herrington, 1962; Clarke, 1981; Taylor, 1981). *Pisidium compressum* (Prime, 1852) was identified at the Dolomite site and might represent the *Pisidium* sp. identified from Point Bartlett. Today it is found throughout North America and has been found as fossils in river, spring, and lake deposits (Bequaert & Miller, 1973). It is found on sandy bottoms, often with submerged vegetation, to depths of 20 m in permanent and perennial waters (Herrington, 1962; Clarke, 1981; Taylor, 1981).

Five species identified from the Point Bartlett site reflect a nearer-shore environment than do the mollusks identified from the Dolomite site. *Gyraulus parvus* and the *Physa* sp. are gastropods that are widely distributed throughout North America (Bequaert & Miller, 1973). *Physa* can tolerate a wide range of water qualities and temperatures. *Physa* and *Gyraulus parvus* both live on dense submerged and emergent vegetation, often in stagnant waters such as ponds and swales (Clarke, 1981; Quade & Pratt, 1989). These species can tolerate seasonal fluctuations in water-level,

but never completely desiccating environments (Taylor, 1981). The lymnaeid and ?*Planorbula* sp. are today found in marshes, seepages, and small streams, and generally can tolerate seasonal desiccation. The ?*Amnicola* sp., if placed in *Fontelicella* (Gregg & Taylor, 1965), reflects a highly vegetated shallow water environment (Taylor, 1981).

Paleoenvironment and Pluvial Lake History

The pluvial lake-level history for Owens Lake has not been assessed, although lake-level records exist for Lake Russell and for Searles Lake, which periodically received overflow from Owens Lake. At Searles Lake, levels were generally intermediate with several oscillations between 23,000 to 10,000 yr B.P. (Benson et al., 1990). Between 15,000 to 13,500 yr B.P., a highstand is inferred. Lake levels dropped to moderately low levels at 13,500 yr B.P., with an intermittently deep condition between 12,500 to 11,500 yr B.P. and perhaps again at 10,500 yr B.P. (Benson et al., 1990). Conditions at Lake Russell reflect intermediate deep-water conditions between 25,000 and 15,000 yr B.P. Records reflect that Lake Russell reached a highstand between 14,500 to 10,000 yr B.P., after which the lake level dropped (Benson et al., 1990).

The periods of highstand and deep-water are probably

related to glacial advances and retreats that occurred in the Sierra Nevada. Radiocarbon dates of $21,000 \pm 130$ (Lebtkin, 1980) from tufa underlying an alluvial fan of inferred Tioga age at Owens Lake (Fullerton, 1986) and $19,050 \pm 210$ yr B.P. on basal rock varnish from an outermost terminal moraine in Pine Creek (Dorn et al., 1987) support a maximum glacial advance before 19,000 yr B.P. (Bursik & Gillespie, 1993). Deglaciation evidence from the west slope of the Sierra Nevada indicates that lower elevations were ice-free after ca. 15,000 yr B.P. (Batchelder, 1980; Edlund & Byrne, 1991; Smith & Anderson, 1992). Deglaciation in the eastern Sierra Nevada is documented by radiocarbon dates from Pine Creek at 13,910 yr B.P. (Dorn et al., 1987) and near the Sierran crest by ca. 12,500 yr B.P. (Anderson, 1990).

Late Pleistocene vegetation records document the widespread occurrence of a Utah juniper (*Juniperus osteosperma*) woodland in Owens Valley (Koehler & Anderson, 1989; Jennings & Elliott-Fisk, 1993; Koehler & Anderson, 1994). The appearance of Mojave Desert understory species at ca. 13,500 yr B.P. indicates warmer conditions than during the full-glacial (Koehler & Anderson, 1994; Koehler & Anderson, unpublished). Reduction of effective moisture in Owens Valley is not recorded until the disappearance of Utah juniper after ca. 9000 yr B.P. (Koehler and Anderson, 1989). Pleistocene megafauna of Owens Valley include mammoth (*Mammuthus* sp.), horse (*Equus* sp.), and camel (*Camelops* sp.) (Jefferson, 1989).

CONCLUSIONS

After the last glacial maxima, Owens Lake reached a highstand, owing to meltwater inundating the Owens River system. This probably occurred between 15,000–13,000 yr B.P. Vegetation records document warming after 13,500 yr B.P. Between 11,000–10,000, wetter conditions (younger Dryas) may have caused Owens Lake to achieve moderate lake levels (Benson et al., 1990). The Dolomite mollusk evidence suggests that the Owens Lake level was at least 1097 m or slightly higher around this time, suggesting low intermediate lake levels. The occurrence of *Physa* and *Gyraulus* at the Point Bartlett site suggests either a shallow bay or marsh environment, as these species can withstand stagnant waters, or that a small nearby stream was flowing into Owens Lake. Evidence from the Dolomite site, such as the presence of the pelecypods and the absence of many species associated with emergent vegetation, implies deeper and cleaner waters. Unfortunately, a paleo-shoreline has not been identified that can be related to the Dolomite assemblage, so that an accurate depth estimate for the assemblage could not be made.

Preservation of the mollusks from the Dolomite site may be attributed to a rapid burial. It would be expected that if a significant drop in lake level caused the local extinction of the molluscan population in this part of the lake, then wave action would cause size grading and disarticulation of the *Anodonta* shells. The pluvial lake history of the

Owens River system records a return to higher lake levels, with Searles Lake reaching deep conditions between 12,500–11,500 yr B.P. (Benson et al., 1989). If the Dolomite date is accurate, periodic or seasonal increased inflow into Owens Lake may have reworked shoreline sediment, burying the assemblage.

The Owens Lake mollusk record is important for understanding the Pleistocene paleoecology of this region. *Helisoma newberryi* and *Vorticifex effusa* were once spread throughout the western pluvial lake system (Taylor, 1985). The pelecypods identified from the Dolomite site suggest an environment that contains permanent and clear waters. The Point Bartlett site yielded a mixed assemblage of species that today are associated with large perennial waters and stagnant and probably vegetated nearshore environment.

ACKNOWLEDGMENTS

I wish to thank Jim I. Mead and R. S. Nittmann for sharing their enthusiasm of mollusks and their help with some of the identifications. Two anonymous reviewers and Barry Roth provided thoughtful and enthusiastic comments that made this paper much more interesting. J. M. Glennon helped in the field collection and curation. Robyn O'Reily drafted the map, and Dan Boone prepared Figure 4. This is Laboratory of Paleocology contribution number 51.

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Fecundity of Female Coral-Inhabiting Snails, *Coralliophila violacea* (Gastropoda: Coralliophilidae)

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Abstract. *Coralliophila violacea* was collected on shallow fringing reefs at Hsiao-liu-chiu, Taiwan, in August 1992. Minimum size of female *C. violacea* with egg capsules was 19.7 mm in shell length. The number of egg capsules observed in the mantle cavity varied from 0 to 8 per female. The mean number of veligers per capsule was 3729. It is known that *C. violacea* inhabits mostly corals of *Porites* spp. A high reproductive potential may be related to host specificity.

INTRODUCTION

The Caribbean snails *Coralliophila abbreviata* (Lamarck, 1816) and *C. caribaea* Abbott, 1958, and the Pacific *C. violacea* (Kiener, 1836) are commonly found on shallow coral reefs. *Coralliophila abbreviata* and *C. violacea* mostly inhabit the surface of living corals, and *C. caribaea* occurs on gorgonians (Ward, 1965; Ott & Lewis, 1972; Robertson, 1980; Miller, 1981; Brawley & Adey, 1982; Soong & Chen, 1991). Usually, coralliophilids aggregate on the surface of corals as patches, but why and how these snails form patches is unknown. Without jaws and radulae (Ward, 1965), they use a well-developed, muscular proboscis to suction-feed on mucus, coelenteron contents, and host tissues (Ward, 1965; Ott & Lewis, 1972; Robertson, 1980; Miller, 1981; Brawley & Adey, 1982). It has been suggested that *C. abbreviata* and *C. violacea* have a life cycle in which there may be a change in sex from male to female (Hayes, 1989; Soong & Chen, 1991). Females retain flat, transparent, chitinous egg capsules in the mantle cavity during early development (Wells & Lalli, 1977; Soong & Chen, 1991). After hatching, veligers of the Caribbean species remain actively swimming and strongly photo-positive for at least 1 week in the laboratory (Wells & Lalli, 1977).

It has been proposed that the fecundity of *Coralliophila violacea* relates to female size (Soong & Chen, 1991) as in protandrous mollusks (Hoagland, 1978). The present study was undertaken to elucidate the relationship between fecundity and female size in *C. violacea*.

MATERIALS AND METHODS

Coralliophila violacea was collected from the surface of *Porites* spp. at depths of 0.5 to 10 m in August 1991 at Hsiao-liu-chiu (southwest Taiwan). Sex of a snail was determined by the presence of a penis or egg capsules. If both characters were present, it was classified as a female. Measurements of shell length, aperture length, and wet tissue weight were determined for females. Egg capsules in the mantle cavity were removed by forceps and preserved in 0.4% formaldehyde. Egg capsules are three-dimensional flat-form packages, but they are ultrathin (ca. 0.016–0.054 mm). Therefore, the size of egg capsules was estimated by the surface area of ellipse, i.e., πAB (where A = the long diameter of ellipse and B = the short diameter of ellipse). After the length and width of capsules were measured with an ocular micrometer, egg capsules were broken to determine the numbers and the size of veligers. Snails were divided into four size classes (12.0–17.9 mm, 18.0–23.9

Table 1

Characteristics of egg capsules produced by females of different size in three species of *Coralliophila* (mean \pm SD).

Species	<i>C. abbreviata</i> *	<i>C. caribaea</i> *	<i>C. violacea</i>
No. of capsules brooded/female	0-4	0-9	0-8
Length of female 12.0-17.9 mm			
Average no. of capsules/female	2.2 \pm 0.7	2.3 \pm 1.4	—
Average no. of embryos/capsule	635.7 \pm 121.3	1977 \pm 360	—
Capsule size in mm ²	19.3 \pm 2.3	16.3 \pm 3.6	—
Embryo density (embryos/mm ²)	32.7 \pm 5.0	121.3 \pm 12.4	—
Embryos/female	1511.4 \pm 354.3	4547 \pm 2889	—
Length of female 18.0-23.9 mm			(11)
Average no. of capsules/female	3.3 \pm 0.5	3.2 \pm 1.3	3.6 \pm 1.7
Average no. of embryos/capsule	886.3 \pm 164.8	3097 \pm 420	2887 \pm 1098
Capsule size in mm ²	28.0 \pm 3.7	26.0 \pm 2.0	34.6 \pm 9.1
Embryo density (embryos/mm ²)	31.5 \pm 4.7	119.1 \pm 16.8	85.4 \pm 10.7
Embryos/female	3034 \pm 526.4	9910 \pm 4257	6508 \pm 5102
Length of female 24.0-29.9 mm			(13)
Average no. of capsules/female	—	4.2 \pm 0.9	4.1 \pm 1.5
Average no. of embryos/capsule	—	3358 \pm 576	4018 \pm 987
Capsule size in mm ²	—	27.0 \pm 5.3	43.6 \pm 10.7
Embryo density (embryos/mm ²)	—	124.4 \pm 20.3	97.2 \pm 18.3
Embryos/female	—	14,100 \pm 3871	9450 \pm 6536
Length of female 30.0-35.9 mm			(4)
Average no. of capsules/female	—	9.0	3.6 \pm 1.1
Average no. of embryos/capsule	—	4658 \pm 294	4952 \pm 1178
Capsule size in mm ²	—	60.0 \pm 2.5	55.8 \pm 11.5
Embryo density (embryos/mm ²)	—	77.6 \pm 3.2	93.0 \pm 15.9
Embryos/female	—	41920	20,419 \pm 488

* Data from Wells & Lalli (1977).

(n) = number of *Coralliophila violacea*.

mm, 24.0-29.9 mm, and 30.0-35.9 mm) to compare characteristics of egg capsules with Caribbean species observed by Wells & Lalli in 1977. Data were analyzed by linear regression (SAS Institute, Inc., 1985).

RESULTS

Twenty-eight *Coralliophila violacea* with 59 egg capsules were examined. Shell length of females with egg capsules ranged from 19.7 to 33.1 mm. Twenty (71.4%) of these snails had both egg capsules and a penis, but penis size was smaller than in males (defined as individuals with penis and no egg capsules). The number of egg capsules in the mantle cavity ranged from 0 to 8 per female. The surface area of an egg capsule among all females varied from 24.1 to 77.4 mm². The number of veligers per capsule among different individuals ranged from 552 to 7492. The shell length of veligers among all females ranged from 0.16 to 0.24 mm. Developmental stages of the larvae within a capsule were similar but different from other consecutive capsules in a single brood. Within the brood from one individual, the number of veligers in a capsule varied from 3101 to 5377.

Positive correlations were found in the relationships between female shell length and wet tissue weight ($y =$

$-0.843 + 0.061x$; $n = 28$; $r = 0.82$, $P < 0.001$), female shell length and average number of veligers per capsule ($y = -2334.7 + 243.6x$; $n = 28$; $r = 0.64$, $P < 0.001$) (Figure 1a), and capsule area vs. number of veligers ($y = 592.5 + 80.4x$; $n = 59$; $r = 0.79$, $P < 0.001$) (Figure 1b). However, the correlation between female shell length and the number of capsules retained per female was not significant ($P > 0.05$).

The minimum size of *C. violacea* with egg capsules was 19.7 mm in shell length (Table 1). The number of capsules in a female were 3.6 in females 18.0-23.9 mm, 4.1 in females 24.0-29.9 mm, and 3.6 in females 30.0-35.9 mm. The number of embryos brooded by females increased with size, averaging from 2887 per capsule in females 18.0-23.9 mm to 4952 in the largest female. Capsule size increased with size of the female, but the density of young in the capsule tended to remain constant. The average number of embryos brooded per female increased with female size from 6508 to 20,419.

DISCUSSION

In *Coralliophila violacea*, female shell length was positively correlated with number of veligers per egg capsule. Thus, our results support the hypothesis that fecundity is size-

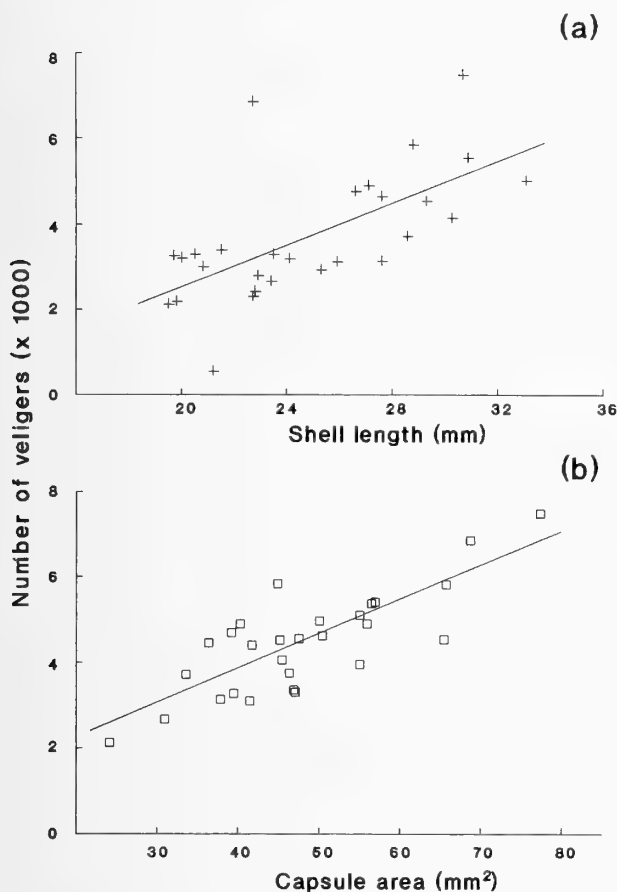


Figure 1

Coralliophila violacea. (a) Relationship between female shell length and average number of veligers per capsule, and (b) egg capsule area vs. number of veligers.

related in this species (Soong & Chen, 1991), as it is in *C. abbreviata* and *C. caribaea* (Wells & Lalli, 1977; Hayes, 1989).

The numbers of egg capsules per female carried by *Coralliophila violacea* ranged from 0 to 8, which is higher than in *C. abbreviata* (0–4 egg capsules), but lower than in *C. caribaea* (0–9 egg capsules) (Table 1). However, a few brooded capsules were released by snails during collection and handling. Therefore, our study slightly underestimates fecundity. Comparatively speaking, the reproductive potential of *C. violacea* is higher than that of *C. abbreviata* and lower than that of *C. caribaea* (Table 1).

Collection of *Coralliophila violacea* indicated that most encapsulated young were in the veliger stage, with only some at earlier developmental stages (personal observation). Although the reproductive season of *C. abbreviata* is unclear, females carrying egg capsules were observed from February to August, but not in December (Ward, 1965; Ott, 1971; Wells & Lalli, 1977). Females of *C. caribaea* with egg capsules were found in July, but the reproductive

season is still unknown (Wells & Lalli, 1977). Therefore, comparisons of fecundity between the two Caribbean coralliophilids were only based on samples collected in August.

Coralliophila abbreviata has a low host specificity and is associated with at least 11 coral species (Abbott, 1958; Ott, 1971; Brawley & Adey, 1982; Hayes, 1989). The host corals include *Acropora palmata*, *A. cervicornis*, *Agaricia tenuifolia*, *A. agaricites* complex, *A. sp.*, *Montastrea annularis*, *Colpophyllia natans*, *C. breviserialis*, *Diploria clivosa*, *D. labyrinthiformis*, and *D. strigosa*. By contrast, *C. caribaea* and *C. violacea* have a high host specificity; the former species mostly inhabits *Gorgonia sp.*, and the latter is found on *Porites* spp. Also, gorgonians are much less common than corals on Caribbean reefs. Although the fecundity of *C. abbreviata* is lower than that of *C. caribaea* and *C. violacea*, the mortality of veligers in *C. caribaea* or *C. violacea* due to inability to locate suitable specific hosts may be much higher than for *C. abbreviata*. This might offset the advantage of high fecundity in *C. caribaea* and *C. violacea* and explain why population density of *C. caribaea* is markedly lower than that of *C. abbreviata* (Wells & Lalli, 1977; Miller, 1981).

ACKNOWLEDGMENTS

We thank Mr. J. L. Chen and Y. W. Chiu for help with collecting coral snails. We also thank Drs. C. M. Lalli and L. L. Liu for constructive criticisms of this manuscript. This study was sponsored by the National Science Council of the Republic of China (NSC 80-0418-B-110-03R). This paper is based on part of a thesis submitted by T. Y. Lin in partial fulfillment of the requirements for the Master of Science degree at Sun Yat-Sen University.

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A Comparative Study of the Functional Morphology of *Semele purpurascens* (Gmelin, 1791) and *Semele proficua* (Pulteney, 1799) (Bivalvia: Semelidae)

by

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Abstract. A comparative study of the functional morphology of *Semele purpurascens* (Gmelin, 1791) and *Semele proficua* (Pulteney, 1799), correlated with the habit and mode of life of both species, was made. Special attention was paid to the siphons, mantle, organs of the pallial cavity, musculature, and alimentary canal. Both species have a mosaic of morphological and ecological aspects, some typical of specialized suspension feeders, others of the deposit-feeding tellinaceans. The behavior of the siphons, the morphology and sorting devices of the organs in the pallial cavity, and the stomach contents reveal a non-selective suspension-feeding habit. According to the most recent view of evolution within the Tellinacea, *S. purpurascens* and *S. proficua* might be classified as representatives of the group considered intermediate in the evolutionary line that proceeds from an early selective suspension-feeding ancestor to the modern and exclusively deposit-feeding Tellinacea.

Details of the organization of the siphonal retractors of a representative of the Tellinacea are given for the first time; the controversy regarding the occurrence of pedal elevator muscles in *Semele* is also discussed. Their presence in the genus is confirmed, although they are more weakly developed and functionally inoperative than those of fast-burrowing Tellinacea.

INTRODUCTION

Semele Schumacher, 1817, the major genus of the Semelidae, is widely distributed in the warm-temperate and tropical waters of the world. The genus is particularly rich in the number of species found in the eastern Pacific, where 28 valid living taxa occur (Coan, 1988). Boss (1972) pointed out its greater abundance in the western Atlantic area during the Tertiary, in contrast to only six species in the Recent fauna. The species are: *Semele purpurascens* (Gmelin, 1791), *S. proficua* (Pulteney, 1799), *S. bellestriata* (Conrad, 1837), *S. nuculoides* (Conrad, 1841), *S. modesta* (Reeve, 1853), and *S. casali* Doello-Jurado, 1949. Of these, *S. purpurascens* is the only species to be present in both Atlantic and Pacific waters, while *S. proficua*, *S. casali*, and *S. bellestriata* have analogous taxa in the eastern Pacific (Coan, 1988).

References to *Semele* species have been found mainly in systematic accounts. Boss (1972) and Coan (1973, 1983, 1988) are the most recent reviewers of the genus in the western Atlantic and eastern Pacific, respectively.

Knowledge of the anatomy of *Semele* is limited. Fischer (1857) gave a brief description of the anatomy of *Amphidesma reticulata* (L.) [sic], referred to *S. proficua* by Coan (1988); Ridewood (1903) analyzed the structure of the ctenidia of *S. orbiculata* (Say, 1822) (= *S. proficua*) and *S. cordiformis* (Holten, 1802); Schröder (1915) described the gross and microscopic morphology of the Chilean *Amphidesma solidum* Gray, 1828 (= *S. solida*); White (1942) offered a discussion on the heart and pericardial gland of *S. sinensis* (A. Adams, 1854) (= *S. cordiformis*); Boss (1972) provided an account of the general gross anatomical features of the genus, based largely on dissections of *S. purpurascens*; and finally, Narchi & Domaneschi (1977) studied the gross morphology of *S. casali*.

Research dealing specifically with the functional anatomy of species of *Semele* is restricted to the ciliary currents on the organs of the pallial cavity of *S. decisa* (Conrad, 1837) by Kellogg (1915), and the study of *S. proficua* by Domaneschi (1982). The papers of Atkins (1937a, b), Yonge (1949), Chapman & Newell (1956), Hughes (1969), Hughes (1973, 1977) deal with aspects of the functional

anatomy of *Abra* and *Scrobicularia*, genera considered representatives of the Semelidae by those authors, as well as by Pohlo (1969). In contrast, Newell (1965), Pohlo (1982), and Keen (1969) recognized the family Scrobiculariidae which includes only the genus *Scrobicularia* (Keen, 1969). Based on the hinge and ligament structures, and on the presence of a posteroventral cruciform muscle and associated sense organ, Morton (1990a) reallocated *Ervilia* from the Mesodesmatidae (Mesodesmatoidea) to the Semelidae (Tellinoidea). Subsequently, Morton (1990b) studied the biology and functional morphology of *Ervilia castanea* (Montagu, 1803) and provided detailed anatomical and biological information about the species.

Based on paleontological data and on the morphology associated with the feeding habits of extant species, including some of *Semele*, Pohlo (1982) made an attempt to expand on the knowledge that he previously (Pohlo, 1967) outlined regarding the evolution within the Tellinoidea, and offered a "more complete evolutionary picture" of these bivalves.

The main purpose of the present paper is to broaden knowledge of the descriptive and functional anatomy of species of *Semele* and correlate it with habitat and life styles. *Semele purpurascens* and *S. proficua* were chosen for this research because they are the most common species of the genus on the coast of São Paulo State, Brazil.

MATERIALS AND METHODS

The examined specimens of *Semele purpurascens* and *S. proficua* came from Barra Velha Beach, Ilha Bela (23°49'S, 45°22.5'W), in the São Paulo State (SP) littoral, Brazil. *Semele proficua* was also obtained from Porchat Island, São Vicente (SP) (23°58'S, 46°22'W). *Semele purpurascens* was never found on Porchat Island.

The structure of the organs, the ciliary currents of feeding and digestion, and other functional aspects of *Semele purpurascens* and *S. proficua* were observed under a stereomicroscope, then compared with each other, and correlated with habitat information.

Drawings of live, relaxed, and preserved specimens were made. Ciliary currents were studied using carmine, Aquadag, and powdered milk suspensions, as well as Carborundum (F), silt, and sand grains. Sections (6 to 10 μ m thick) were made of specimens fixed in Bouin's fluid and stained with acid fuchsin and Mallory's triple stain.

Living specimens were observed at the Department of Zoology, Bioscience Institute, University of São Paulo, where the animals were kept alive, buried by themselves in clean sand, and fed on suspended organic detritus, yeast, and powdered milk, for periods of up to 6 months.

MODE OF LIFE

Semele purpurascens and *S. proficua* are sympatric in many places of their distribution in the western Atlantic. *Semele purpurascens* occurs from Cape Fear, North Carolina, to

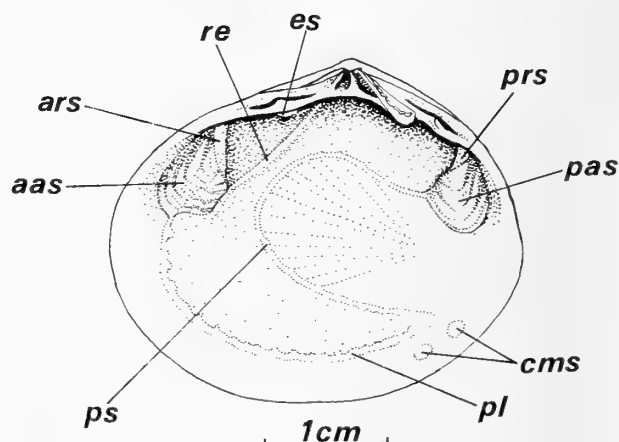


Figure 1

Semele purpurascens. Internal view of the right shell valve. **aas**, anterior adductor muscle scar; **ars**, anterior pedal retractor muscle scar; **cms**, cruciform muscle scar; **es**, pedal elevator muscle scar; **pas**, posterior adductor muscle scar; **pl**, pallial line; **prs**, posterior pedal retractor muscle scar; **ps**, pallial sinus; **re**, radial elevation.

Rio de la Plata, Uruguay, from shallow water to 630 meters in depth (Boss, 1972). *Semele proficua* occurs from Beaufort, North Carolina, south to Isla Leones, Argentina, from shallow water to a depth of 75 meters, buried in sand, sandy mud, and sand among rocks (Boss, 1972; Rios, 1985).

In the São Paulo State littoral, both species inhabit quiet waters with low amounts of suspended mineral particles. They are sympatric in Barra Velha Beach, Ilha Bela, where they live buried in a grassy, sand mud bottom, among the roots of the sea grass *Halodule wrightii*. In this particular habitat, the bottom surface is exposed only during extremely low tide. All specimens were found lying on their left side within the substrate, the hingeline usually within 30°–45° in relation to the horizontal. They were located no more than 5 centimeters below the surface, where the sediment is lighter in color than the underlying anoxic substrate. These species are not sympatric in Porchat Island, São Vicente, where only *S. proficua* was found. Here, *S. proficua* lives buried in small basins of sandy mud formed among boulders in the intertidal zone. In this locality, Domaneschi (1982) found the largest studied specimen (3.80 cm in length) buried to a depth of 11 centimeters.

RESULTS

The Shell

Boss (1972) presented a detailed description of the valves of *Semele purpurascens* and *S. proficua*. An internal view of the right valve of *S. purpurascens* is shown in Figure 1. Domaneschi (1982) also described and illustrated the shell of *S. proficua*.

Despite his detailed treatment, Boss (1972) made no

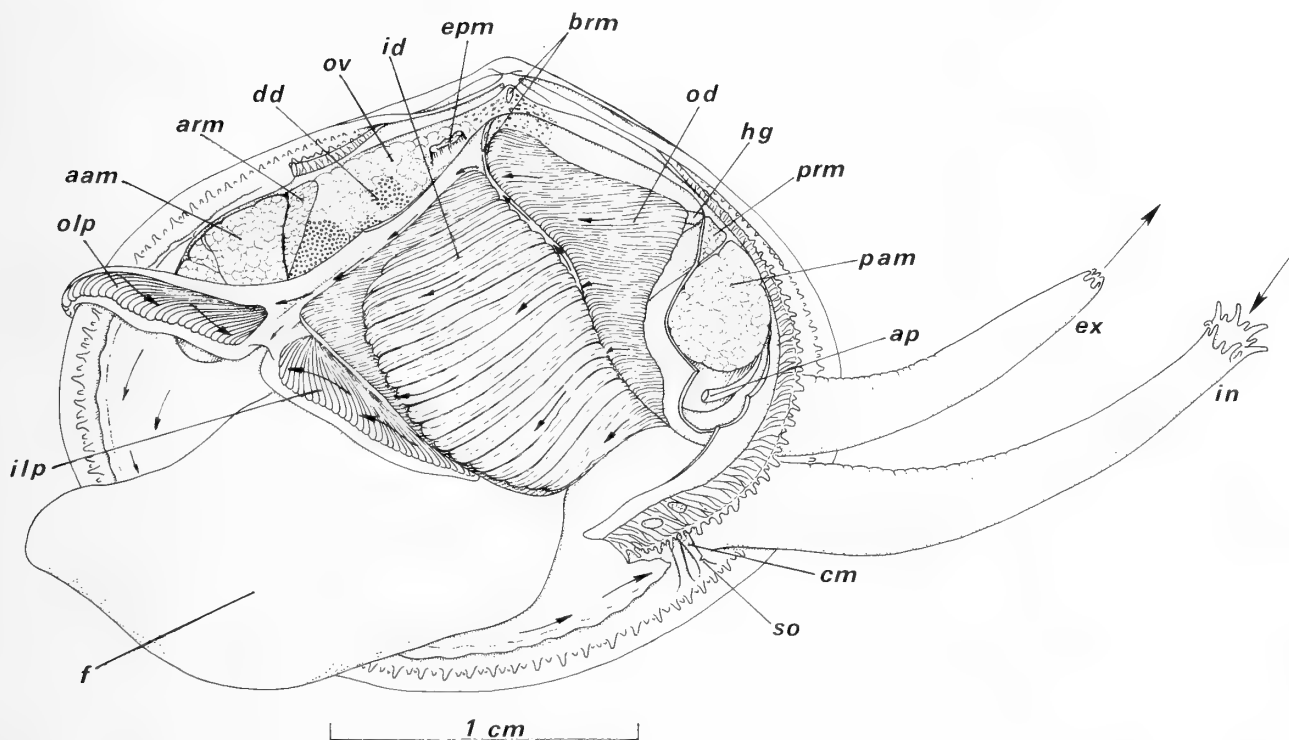


Figure 2

Semele purpurascens. The organs of the pallial cavity viewed from the left side after removal of the left shell valve and mantle lobe. **aam**, anterior adductor muscle; **ap**, anal papilla; **arm**, anterior pedal retractor muscle; **brm**, branchial retractor muscle; **cm**, cruciform muscle; **dd**, digestive diverticula; **id**, inner demibranch; **epm**, elevator pedal muscle; **ex**, exhalant siphon; **f**, foot; **hg**, hind-gut; **ilp**, inner labial palp; **in**, inhalant siphon; **od**, outer demibranch; **olp**, outer labial palp; **ov**, ovary; **pam**, posterior adductor muscle; **prm**, posterior pedal retractor muscle; **so**, sensorial organ.

reference to the scar of the branchial retractor, or to that of the pedal elevator muscle. The first scar is located deep in the umbonal cavity and is conspicuous in most of the specimens. The second scar (Figure 1, **es**) is located near the base of the anterior lateral tooth as a single or subdivided impression, often irregular in outline. Coan (1973) delineated a scar in the shell figures of *Semele decisa*, *S. rubropicta* Dall, 1871, *S. incongrua* Carpenter, 1864, and *S. pulchra* (Sowerby, in Broderip & Sowerby, 1832) at the same position where the pedal elevator muscle scar of *S. purpurascens* and *S. proficua* is found.

Although the shell is considered equivalve, the valves of *Semele purpurascens* and *S. proficua* show some asymmetry. The posterior end exhibits a slight curvature to the right, accompanied by a radially arranged slight depression on the outer surface of the left valve and a corresponding elevation on the right valve. These shell characters, absent in the early juvenile stage, become more and more conspicuous as the animal grows older. Holme (1961) reported a similar posterior flexure of the shell valves of some Telinidae.

The Mantle

Boss (1972), Narchi & Domaneschi (1977), and Domaneschi (1982) have given a detailed picture of the mantle in species of *Semele*. Boss (1972) stated that "along the margins" of the mantle lobes of *S. purpurascens* there are "short tentacles developed on the middle fold." A detailed observation of this species revealed not only short tentacles along the middle fold but, as observed by Narchi & Domaneschi (1977) in *S. casali* and by Domaneschi (1982) in *S. proficua*, they are of different sizes and disposed in three rows. The longer tentacles are located internally; those on the middle row are less developed and alternate, one by one, with the longer tentacles; the smallest tentacles form the third, external row.

In quiescent specimens of *Semele purpurascens* and *S. proficua*, when foot and siphons are withdrawn, the free edge of the mantle folds are kept in contact except for a short extent along the pedal gape, allowing an incurrent flow of water into the pallial cavity. Another gape occurs at the point of emergence of the siphons, allowing the water

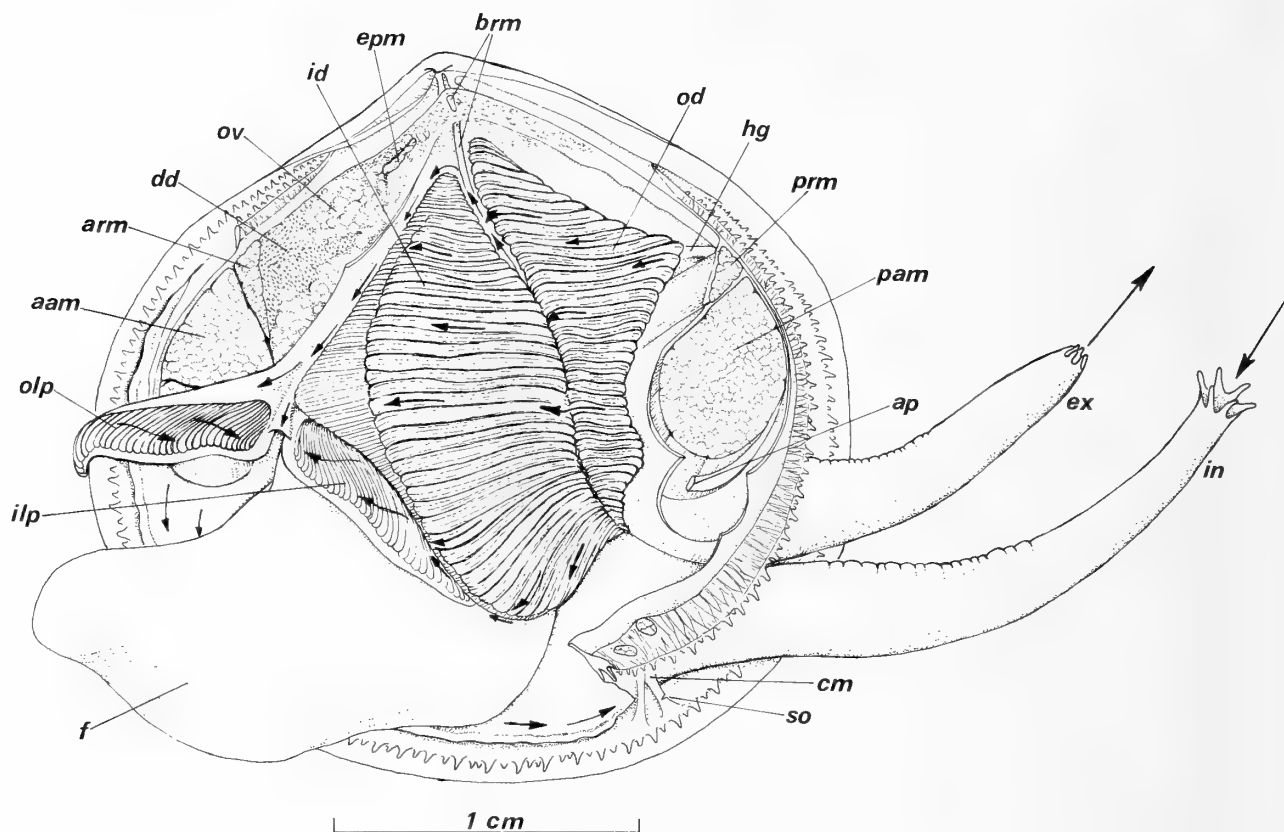


Figure 3

Semele proficua. Lettering as in Figure 2. (Redrawn after Domaneschi, 1982.)

to flow out of the animal. On the incurrent aperture along the pedal gape, extended tentacles interlock loosely, forming a feeble barrier against the entrance of large particles; on the excurrent aperture, extended tentacles stand outward. In animals where the foot and/or the siphons are protruded, extended tentacles surround these organs and, touching them closely, prevent adhering particles from being drawn into the pallial or siphonal cavity, respectively, as the organs retract.

The mantle lobes of *Semele purpurascens* and *S. proficua* lack the additional fold which isolates the rejection channel for pseudofeces (waste canal of Kellogg, 1915) present in some of the Tellinidae and Semelidae studied by Yonge (1949).

Siphons

The siphons of *Semele purpurascens* and *S. proficua* (Figures 2, 3) are long and separate (type A of Yonge, 1948, 1982). The inhalant siphon extends to lengths of up to 4 times the shell length in the former species and to $4\frac{1}{2}$ times in the latter. The exhalant siphon extends up to 3 times the shell length in both species.

In *Semele purpurascens*, the inhalant aperture is fringed with one ring of 12 simple fingerlike tentacles, six of which are more developed and alternate regularly with six shorter tentacles. The exhalant aperture is fringed with only six short fingerlike tentacles. Both siphons of *S. proficua* bear one ring of six simple, equally developed tentacles; those on the inhalant opening being longer (Domaneschi, 1982).

Specimens of *Semele purpurascens* and *S. proficua* buried in aquaria remain for a long time in the same place; horizontal migration was never observed. The pebbles and sea grass roots present in the natural substratum of the species might limit their movements and impose a sedentary mode of life. Such animals protruded the inhalant siphon obliquely through the substratum, keeping the opening well clear of the bottom surface or a little above or below it.

When extruded from the substratum, the inhalant siphon is held passively for a long time with the ring of tentacles curled outward slightly, exposing a trumpet-shaped opening and permitting suspended material to pass freely into the pallial cavity. In this situation, the only movements observed were sporadic circular constrictions running down to the base; during such episodes, the siphon

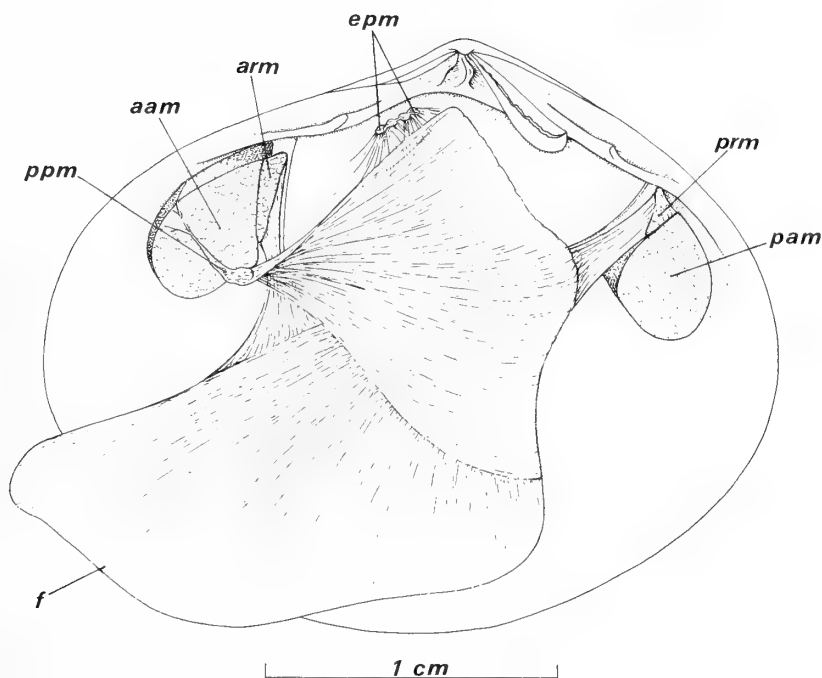


Figure 4

Semele purpurascens. The arrangement of the musculature. **aam**, anterior adductor muscle; **arm**, anterior pedal retractor muscle; **epm**, elevator pedal muscle; **f**, foot; **pam**, posterior adductor muscle; **ppm**, pedal protractor muscle; **prm**, posterior pedal retractor muscle.

extends upward, elongates, and then produces a sudden whiplike movement which throws pseudofeces far from the animal. The inhalant siphon was never seen bending down onto or along the bottom sediment sucking in deposited material as in typical deposit-feeding tellinaceans described by Yonge (1949).

When the inhalant aperture of *Semele purpurascens* and *S. proficua* is kept at the level of or below the bottom sediment, the tentacles can be directed toward the opening, thus reducing the entrance of large particles into the pallial cavity. Sources of these large particles include suspended particles in the water column and dense ones lifted from the bottom, pulled in by the inhalant water current. Benthic organisms and other particles deposited around the siphonal hole in the sediment can precipitate passively, and fall into the siphonal opening.

Contrary to what was observed by Domaneschi (1982) for *Semele proficua*, buried specimens of *S. purpurascens* rarely exposed the exhalant opening directly into the water column; of 100 living specimens kept buried in aquaria, only three exposed their exhalant openings. Specimens of *S. proficua* buried close to the aquaria walls could be seen eliminating feces into the sand grain interstices as the exhalant siphons were extruded through the sediment. As the siphonal aperture emerges into the water column, the fecal pellets, united with each other as a string of beads, are deposited on the bottom surface around the siphonal

hole in the sediment. Observations of *S. purpurascens* offered no similar opportunities.

A flash of light evoked in both species a sudden retraction of the siphons but with little modification in their length and diameter. Shading caused no reactions. Sudden retraction of the siphons into the sediment or into the shell valves was caused by vibrations in the aquaria or in the dish where the animals were buried. The displacement of the sand grains in the vicinity of the siphons, as well as mechanical stimulus with a pin, caused the same results.

Musculature

The general muscular systems of *Semele purpurascens* and *S. proficua* are shown in Figures 4, 5 and 6.

Adductors. The adductors (Figure 4; **aam**, **pam**) are unequal and ovate, the anterior being more developed than the posterior, particularly in *Semele purpurascens*.

Pedal musculature. The extrinsic pedal musculature (Figure 4) consists of bilateral pairs of anterior (**arm**) and posterior (**prm**) pedal retractors, one pair of anterior pedal protractors (**ppm**), and one pair of vestigial pedal elevator muscles (**epm**).

The anterior pedal retractor is attached to the shell by an elongate triangular insertion, adjacent and posterior to that of the anterior adductor. Thence, the majority of the

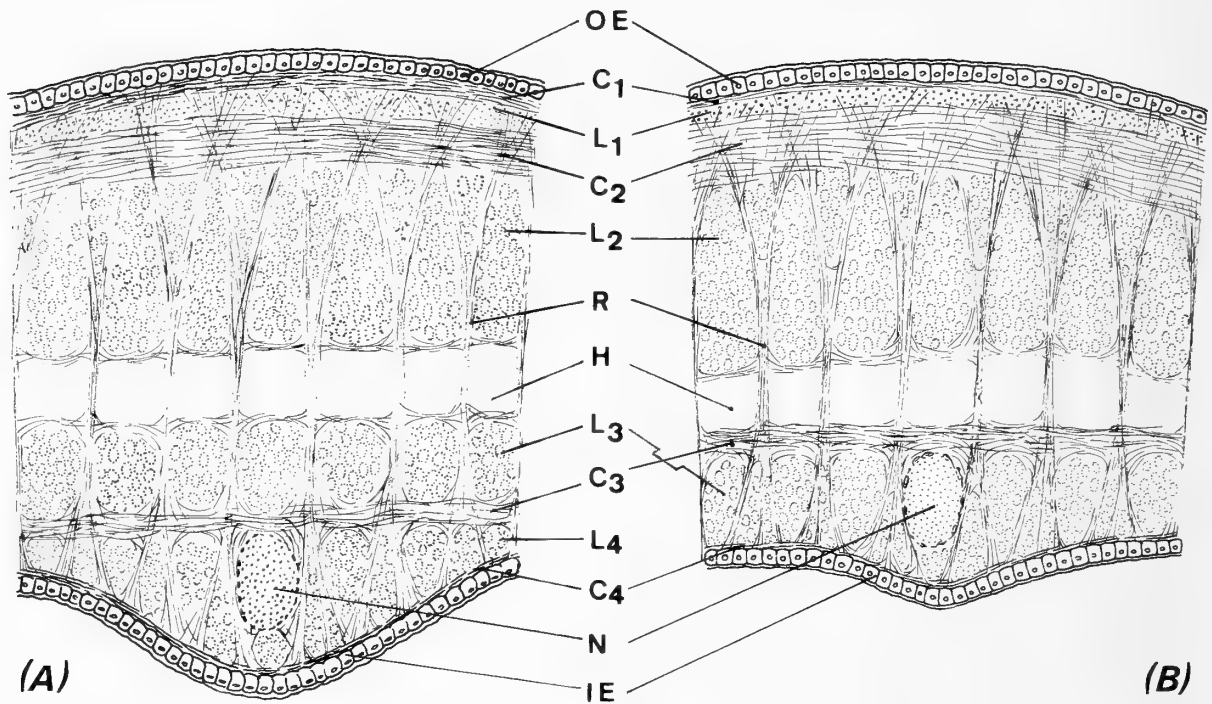


Figure 5

Intrinsic musculature of the siphonal walls (cross section). A and B, inhalant siphon of *Semele proficua* and *S. purpurascens*, respectively. C₁ to C₄, circular layers; H, blood spaces; IE, inner epithelium; L₁ to L₄, longitudinal layers; N, nerve cord; OE, outer epithelium; R, radially arranged muscles strands. (A, redrawn after Domaneschi, 1982.)

fibers from the right and the left muscles pass almost vertically and separately into the foot, where they form the innermost muscular layer, on the corresponding side of the organ. Only the bundles proceeding from the internal side of the triangular insertion of each muscle converge in the sagittal plane of the animal, the right bundles crisscrossing with those coming from the left, as they enter the foot and vice versa.

The posterior pedal retractor muscle attaches to the shell valves by a less elongated triangular insertion lying dorsal in relation to the posterior adductor. The right and left posterior pedal retractors proceed anteriorly, converging in the sagittal plane, and fuse just beneath the kidney, forming a thick, median bundle. Here, the bundles of fibers intersect and split; the fibers coming from the right pass deeply into the left side of the foot and vice versa, where they form, in the corresponding side of the organ, an outer layer in relation to the fibers of the anterior pedal retractor.

In both species, the pedal protractor muscle, on each side, traverses the anterior adductor muscle completely, from its posteroventral side to the anterodorsal, and inserts on the shell valves with the adductor. In a few specimens, the adductor muscle was not so conspicuously divided into anterior and posterior halves, because the protractor was observed to narrow abruptly to a continuous or discontin-

uous thin lamina. Boss (1972) might have based his observations on such specimens to prepare his "anatomical notes" and "Plate 3" where indications of a completely divided adductor are not found.

From its insertion on the shell valve, the well-developed pedal protractor runs posteriorly, twists abruptly as it enters the foot and, then, spreading fanwise, forms a third muscular layer; this constitutes the outermost layer into the foot, in relation to those of the posterior and anterior pedal retractors.

Contrary to what was stated by Boss (1972), a pedal elevator muscle is present on each side of *Semele purpurascens*. According to Domaneschi (1982), that muscle also occurs in *S. proficua*. In both species, the pedal elevator muscle is formed by a number of short fibers that emerge from the roof of the visceral mass and insert on the shell ventral to the anterior lateral tooth. The presence of this muscle can be easily overlooked in living or preserved specimens removed from the shell. Nevertheless, the well-impressed scar on the shell valves announces its existence, as well as the fact that its fibers can join in a single or multiple bundles. Careful dissections and translucent preparations were not sufficient to determine the position of the fibers of the pedal elevator muscles in relation to other muscle layers into the foot.

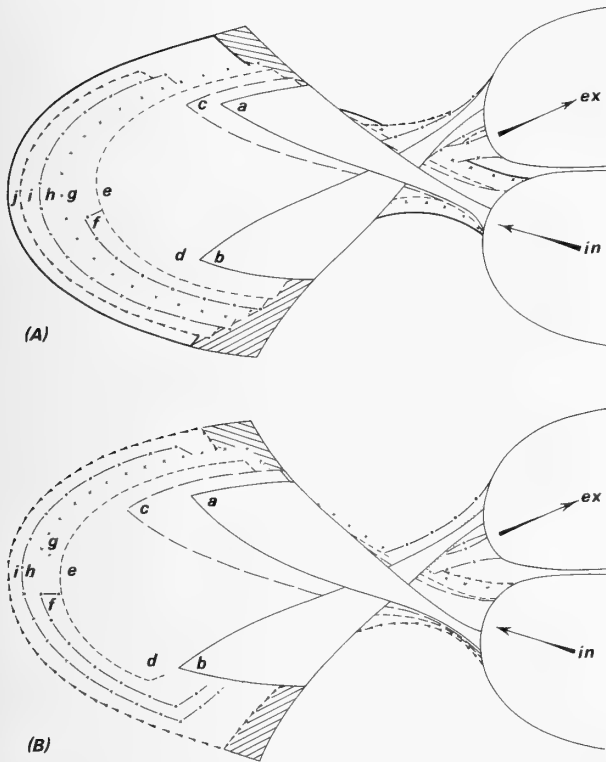


Figure 6

Semi-diagrammatic representation of the left siphonal retractor muscle, seen from the outer to the inner face, to show the origin, sequence and angularity of its fan-shaped muscular layers. Only the inner layer is shown in its full extension. A, *Semele purpurascens* (a, c, e, g, j) and (b, d, f, h, i), layers coming from the inhalant and exhalant siphons, respectively. B, *S. proficua* (a, c, e, g, i) and (b, d, f, h), layers coming from the inhalant and exhalant siphons, respectively.

Apart from the extrinsic pedal muscles, the visceral part of the foot of *Semele purpurascens* and *S. proficua* contains a thin sheet of circular fibers located just beneath the epithelium, and a large number of small, isolated bundles of transverse muscle fibers. These bundles pass between the coils of the intestine and the diverticula of the digestive glands and the gonads, inserting on the muscular wall on each side of the foot.

Cruciform muscle. The cruciform muscle (Figures 2, 3; **cm**) with its specialized sensory organ (**so**) occurs slightly anterior to the point of origin of the inhalant siphon and immediately ventral to the embayment in which waste matter is collected prior to ejection from the mantle cavity.

The arrangement of the cruciform muscle and its associated sense organ is the same in *Semele purpurascens* and *S. proficua*. The slitlike space which stretches completely across each posterior half of the cruciform muscle is closed everywhere, except postero-ventrally where it communicates with a somewhat spherical ciliated cavity,

the sense organ. This organ opens directly to the siphonal space, the opening being at the summit of a minute elevation visible under a light microscope.

Siphonal musculature. In both siphons of *Semele purpurascens*, the siphonal musculature (Figure 5B) is arranged, from the outer to the inner epithelium, in the following muscle layers: (1) thin circular (C_1); (2) thin outer longitudinal (L_1) made up of isolated fibers; (3) thick circular (C_2); (4) massive longitudinal (L_2) containing groups of fibers; (5) third circular (C_3), which is less thickened than " C_2 "; (6) third longitudinal (L_3), which has the same characteristics of " L_2 ," but is less developed especially in the exhalant, and finally, (7) a thin circular (C_4), detected only in the inhalant siphon. The exhalant siphon of *S. purpurascens* thus has six muscle layers. Radially arranged muscle strands (**R**) run from one epithelium to the other, separating the longitudinal muscle layers " L_2 " and " L_3 " into a series of sharply defined bundles. A series of blood spaces (**H**) is circumscribed by the longitudinal (L_2) and circular (C_3) layers and by the radially arranged strands.

The exhalant siphon of *Semele proficua* has exactly the same six muscle layers described for the exhalant siphon of *S. purpurascens*. The inhalant siphon of *S. proficua* (Figure 5A) differs from that of *S. purpurascens* in a few aspects: (1) in *S. proficua* there are two thick longitudinal layers running between the circular " C_2 " and " C_3 " vs. only one in *S. purpurascens*; (2) its longitudinal layer " L_4 ," corresponding in position to " L_3 " in *S. purpurascens*, is grouped into well-defined bundles only in the vicinity of the nerve cords (**N**), with sparse fibers in the interspace between the nerves; (3) its blood spaces are situated between two longitudinal muscle layers.

As described by Domaneschi (1982) for *Semele proficua*, bundles of fibers derived from the longitudinal muscle layers, especially those located between the circular " C_2 " and " C_3 ," emerge laterally from the base of both siphons of *S. purpurascens* to form the siphonal retractor muscles (Figure 6). Each bundle flattens to a thin lamina as it leaves the siphon, then its fibers spread out to form a little "fan." The angularity varies among different "fans" in a same siphonal retractor.

Careful dissection of at least 10 siphonal retractors of each species revealed that at a short distance from the base of the siphons, the bundles emerging from the exhalant interpose almost regularly, one by one, between those coming from the inhalant siphon, giving a stratified appearance to the narrower region of the retractor. Several bundles of fibers were detected, and their relative position from the outer to the inner epithelium of the mantle and to what extent each bundle contributes to the general organization of the fan-shaped siphonal retractor is illustrated in Figure 6.

The Mantle Cavity

The organs in the mantle cavity of *Semele purpurascens* and *S. proficua* are shown in Figures 2 and 3. The major features of the different organs are outlined below.

Table 1

Anatomical data relative to the inner demibranch of specimens measuring 20 mm in length.

Species	Plicae (total no.)	Deepest plicae (mm)	Filaments/plicae inner demibranch		
			Minimum	Maximum	Average
<i>S. purpurascens</i>	16	0.5	11	30	21
<i>S. proficua</i>	28	0.5	09	33	22

Ctenidia. The outer demibranch (**od**) is reduced to a single inner (descending) upturned lamella, leaving the inner demibranch (**id**) uncovered; the inner demibranch is complete in having outer (descending) and inner (ascending) lamellae (Figure 7).

A reflected lamella, corresponding to the remainder of the originally ascending lamella, as proposed by Ridewood (1903) for the species of *Tellina* he studied, is lacking in the outer demibranch of *Semele purpurascens* and *S. proficua*.

Contrary to the view of Boss (1972) about the outer demibranch of *Semele purpurascens*, the present study revealed that this organ in this species is completely smooth like that of *S. casali* studied by Narchi & Domaneschi (1977). Living specimens show transitory undulations on the outer demibranch caused by its intrinsic musculature. This feature may be retained in preserved specimens and must not be confused with typical folds. The outer demibranch is deeply folded in *S. proficua* (Domaneschi, 1982). This same condition was recorded by Ridewood (1903) for *S. orbiculata* (= *S. proficua*) and *S. cordiformis* and by Kellogg (1915) for *S. decisa*.

The inner demibranchs of *S. purpurascens* (Figure 8A) and *S. proficua* are deeply plicated. In the first species, the plicae are generally less numerous than in the second species (Table 1). The filaments at the bottom of the trough between two successive plicae are so barely differentiated from ordinary ones (**f**) on the plicae that it is difficult to identify one that could be characterized as principal, according to Ridewood's (1903) concept. In histological sections, the most central filament in the troughs may be distinguished either by its wider base or its more developed chitin-band, or both. Occasionally, that filament is the only one associated with the interlamellar junction septum (**ij**). Ridewood (1903) also referred to weakly differentiated principal filaments in *S. orbiculata* (= *S. proficua*) and *S. cordiformis*.

The plicae in both species compared here tend to smooth out toward the free margin of the inner demibranch, because of the largely fused filaments, giving rise to a smooth marginal area. This smooth area is markedly triangular in shape, where it is inserted between the labial palps. The distal ends of the filaments that form the anterodorsal half of that triangular smooth area are inserted into and

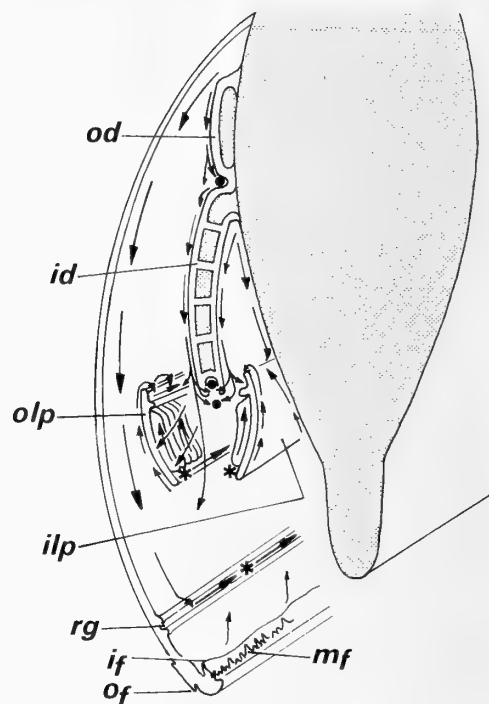


Figure 7

Semele purpurascens and *S. proficua*. Diagrammatic vertical section through the body to show the dynamics of the ciliary currents on the right half of the pallial cavity. The anterior end is toward the left. **id**, inner demibranch; **if**, inner mantle fold; **ilp**, inner labial palp; **mf**, middle mantle fold; **od**, outer demibranch; **of**, outer mantle fold; **olp**, outer labial palp; **rg**, rejection groove. ●, oralward currents; *, posteriorly directed rejection currents. (Redrawn after Domaneschi, 1982.)

fused to a distal oral groove (category II of Stasek, 1963) (Figure 9). The free tip of the remaining filaments forms the lateral walls of a conspicuous and evenly deep (50 μ m) marginal food groove.

The filaments of both demibranchs (Figure 8B, Table 2) are endowed with lateral (**lc**), laterofrontal (**lfc**), and frontal (**fc**) cilia. Toward the free distal end of the filaments of the inner demibranch, the frontal cilia are replaced by increasingly longer terminal cilia. The rows of specialized

Table 2

Types of cilia present in the inner demibranch and their respective lengths. **fc**, frontal cilia; **gc**, guard-cilia; **lc**, lateral cilia; **lfc**, laterofrontal cilia; **tc**, terminal cilia.

Species	Cilia				
	lfc (μ m)	fc (μ m)	lc (μ m)	tc (μ m)	gc (μ m)
<i>S. purpurascens</i>	16.0	2.4	10.0	38.0	62.0
<i>S. proficua</i>	22.0	2.0	10.0	36.0	54.0

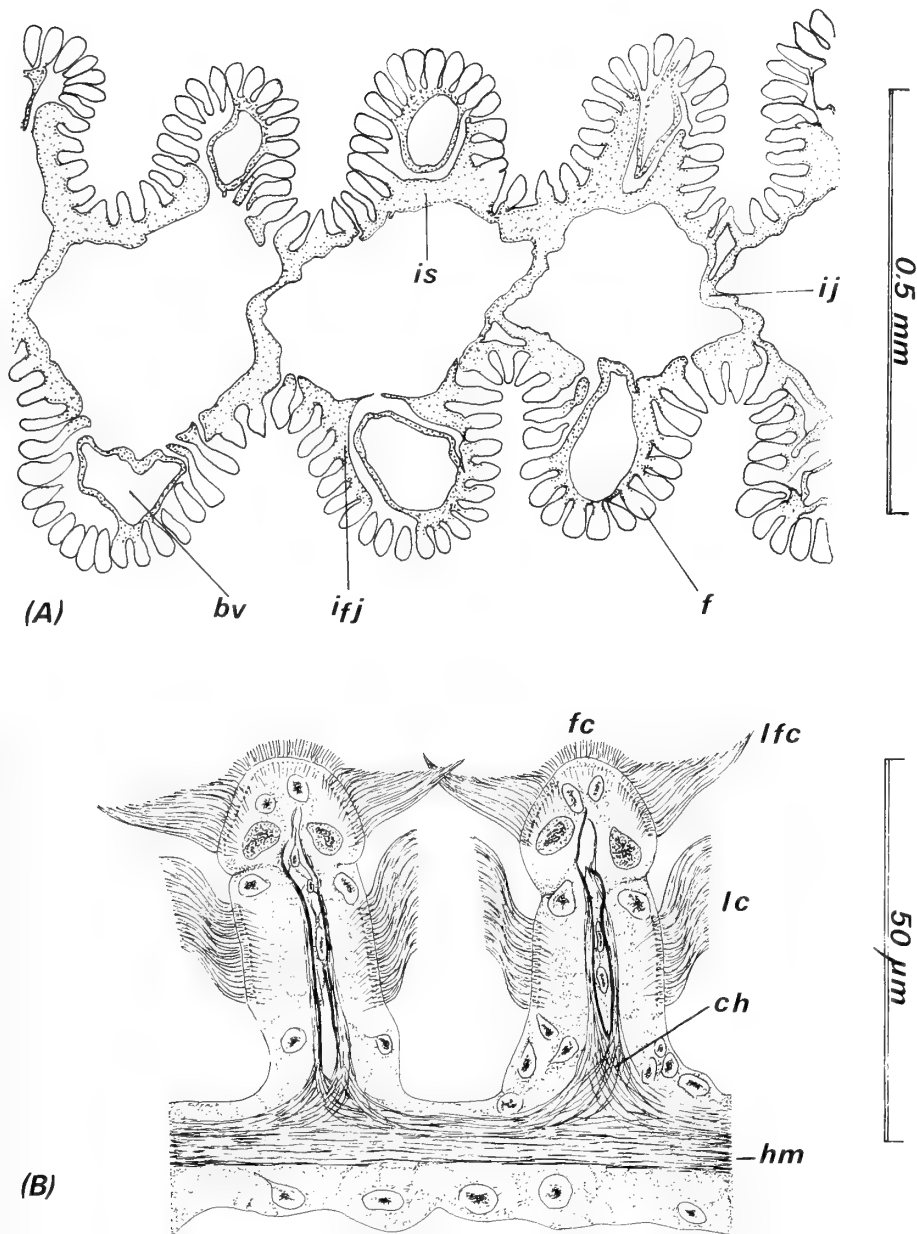


Figure 8

Semele purpurascens. Cross sections through the inner demibranch (A), and through two filaments of the same (B). **bv**, blood vessel; **ch**, chitin; **f**, filament; **fc**, frontal cilia; **hm**, horizontal muscle; **ifj**, interfilamentar junction septum; **ij**, interlamellar junction septum; **is**, intraplacial septum; **lc**, lateral cilia; **lfc**, laterofrontal cilia.

cirruslike frontal cilia, to which Atkins (1937a) attributed the function of increasing the inhalant current caused by the small ctenidia of *Abra* and *Scrobicularia*, were not found in *Semele purpurascens* and *S. proficua*. These last two species also lack another type of specialized large frontal cilia present in *Abra* to which Atkins (1937a) attributed the function of removal of unwanted material, such as sand grains, from the ctenidia. On the other hand, *S. purpur-*

ascens and *S. proficua* have groups of long, fan-shaped, fairly fine and flexible cilia transversely inserted on the inner side of each filamentar lobe of the marginal groove, not present in *Abra* and *Scrobicularia*. These cilia, named guard-cilia by Atkins (1937a), are inserted in the lobe almost at a right angle to the filamentar axis, as in *Aloidis* (*Corbula*) *gibba* (Olivi, 1792) (Yonge, 1946). The fan-shaped groups of guard-cilia isolate a channel in the depth

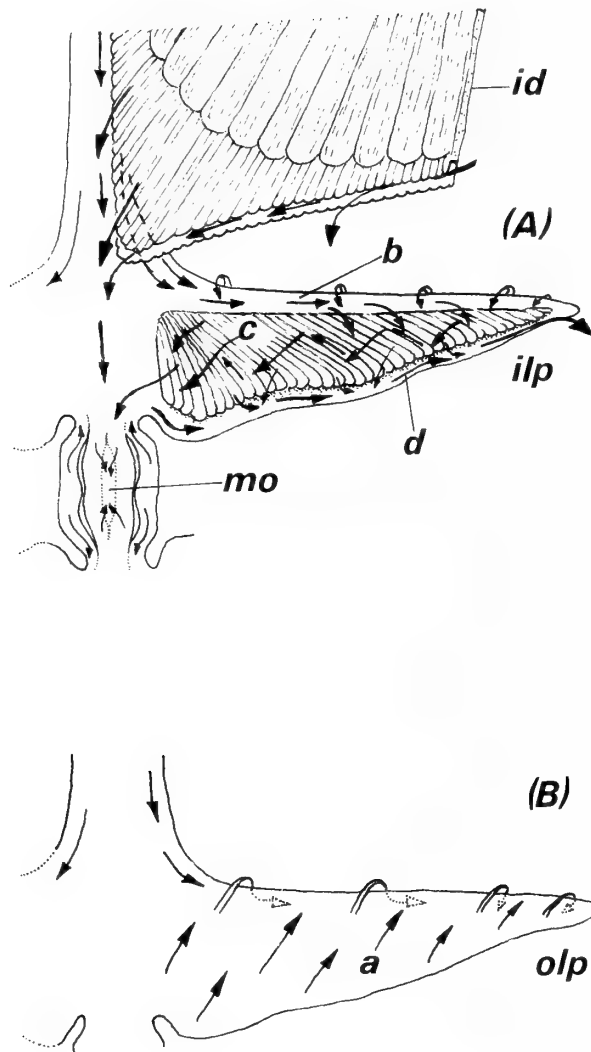


Figure 9

Semele purpurascens. Left labial palps viewed from the folded (A) and smooth (B) surfaces. The arrows show the path taken by the particles. In A, the mouth was turned aside from its original position to show acceptance and rejection currents around it. **id**, inner demibranch; **ilp**, inner labial palp; **mo**, mouth; **olp**, outer labial palp. For lettering (a), (b), (c), (d), see text.

of the marginal groove from a superficial channel bordered by the coarse terminal cilia.

Figures 2, 3, and 7 show the ciliary currents of the ctenidia. On the outer demibranch of *Semele purpurascens*, as also observed by Domaneschi (1982) for *S. proficua*, the frontal currents convey material toward the ctenidial axis where a very active oralward current is present.

The intrinsic musculature of the ctenidial axis of *Semele purpurascens* and *S. proficua* is responsible for causing the proximal region of the two demibranchs of each side to move toward and away from one another, exposing and

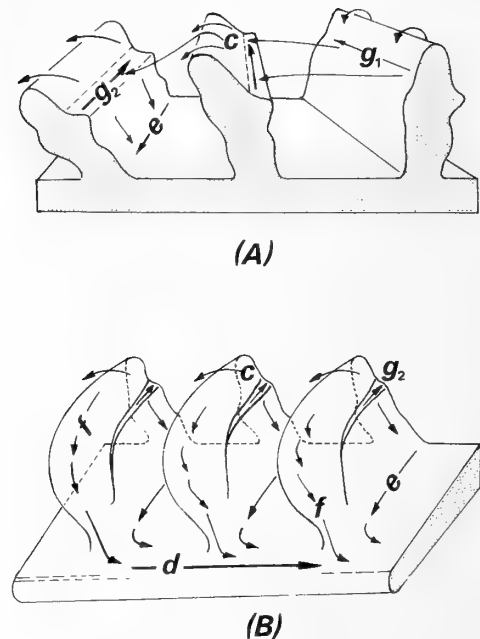


Figure 11

Semele purpurascens and *S. proficua*. Diagram of the ciliary mechanisms on the folded surface of the labial palp, to show the various ciliary tracts. The dorsal margin is toward the top, the anterior to the left. A and B represent sections from a median and from a free distal portion of the folds, respectively (redrawn after Domaneschi, 1982). For lettering (c), (d), (e), (f), (g₁), (g₂), see text.

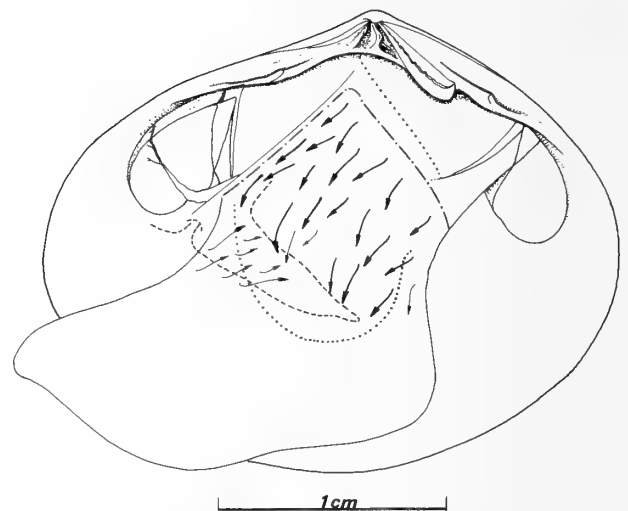


Figure 10

Semele purpurascens. Ciliary currents on the left side of the visceral mass. [.....] ventral and dorsal limits of the visceral mass; [-----] area of the visceral mass juxtaposed with the inner labial palp; [- - - -] line of insertion of the ascending lamella of the inner demibranch with the visceral mass.

hiding the axial groove. The posterior region of the outer demibranch can and does bend over, well down toward the axial groove, touching the filaments of the inner demibranch. These mechanisms regulate the quantity and the size of particles that can reach the axial groove; they also prevent clogging in the hind area of the ctenidia if turbid water enters the pallial cavity through the inhalant siphon.

On both lamellae of the inner demibranch of *Semele purpurascens*, the frontal currents are exclusively toward the marginal food groove, both in the troughs and on the crests of the plicae. On the anterior third of the outer lamella, collected material is carried toward the distal oral groove where it meets the material coming from the ctenidial axis and travels outward; on the anterior third of the inner lamella, particles are conveyed to the inner labial palp (Figure 9A).

Particles reaching the free edge of the inner demibranch are submitted to sorting mechanisms by coarse cirruslike terminal cilia flanked by fine frontal cilia and by the marginal groove provided with guard-cilia. Fine particles are carried by the frontal cilia into the depth of the marginal food groove, where they have a safe passage to the mouth, aggregated in a thin mucous strand. Large particles and mucous strands transported precariously by the coarse terminal cilia outside the food groove are usually rejected. The lateral walls of the marginal food groove were seen moving toward and away one from another, acting as a sorting mechanism; coming near, the tips of the opposite fan-shaped groups of guard-cilia touch one another, creating an efficient barrier against the entrance of large particles; spreading outward, the groove opens fairly widely, but the stiff guard-cilia arched above still prevent the entering of material, except for isolated particles or thin mucous strands. When the marginal groove is wide open, mucous strands running inside it can move out and be passed to the labial palps or can be rejected to the mantle. Purchon (1963) described a similar sorting device involving the marginal food groove for the donacid *Egeria radiata* (Lamarck, 1804).

On each side of the body of *Semele purpurascens* and *S. proficua*, there are two oralward currents: one on the ctenidial axis and another on the groove along the free edge of the inner demibranch (Figure 7); the ciliary currents on their demibranchs belong to type E(a) as described by Atkins (1937b).

The visceral mass and the foot. Despite its dense ciliated epithelium, no ciliary activity could be detected on the surface of the foot of both species. The ciliary currents over the visceral mass of *Semele purpurascens* do not differ significantly from those illustrated by Domaneschi (1982) for *S. proficua*. Over the visceral mass of *S. purpurascens*, ventrally directed currents (Figure 10) carry particles onto the area covered by the smooth outer face of the inner labial palp and by the free edge of the inner demibranch. Dorsalward currents are present over the surface of the

visceral mass juxtaposed with the inner labial palp. Both currents converge particles which are then caught by the ciliary tracts on the smooth outer face of the inner labial palp; from here, they are conveyed to the dorsal margin and then passed to the inner folded surface of the palp to be sorted. Particles reaching the posterior region of the visceral mass are cleared by the tip of the labial palp or by the cilia on the free edge of the inner demibranch; some of these particles were seen being passed to the rejection tracts on the mantle.

The labial palps. The labial palps of *Semele purpurascens* and *S. proficua* have a length of about one-third that of the animal's shell, and differ only in some functional aspects pointed out below. The structure and ciliary sorting mechanisms of the palps of *S. purpurascens* are shown in Figures 9 and 11. The following ciliary currents were observed:

(1) transversely dorsalward currents (a), on the smooth outer surface, convey particles onto the folded inner surface.

(2) longitudinal current (b), on the smooth dorsal margin of the inner surface. Midway to the tip of the organ, particles are passed onto the folds in *S. purpurascens*; in *S. proficua* they are carried onto the tip, whence they are thrown over the folds.

(3) transversely directed currents (c), operating obliquely oralward and markedly ventralward across the folds, act as either acceptance or rejection currents, depending upon the size or total volume of particles.

(4) rejection current (d), on the smooth ventral margin of the inner surface, carrying particles to the tip of the palp, thence throwing them off to the mantle.

(5) rejection currents (e), on the floor of the grooves between adjacent folds, driving particles to the rejection current "d."

(6) rejection currents (f), on the free distal end of the folds, driving particles toward rejection current "d."

(7) dorsalward re-sorting currents (g₁, g₂), along the entire extent of both faces of each fold:

g₁—on the adoral face of the fold, dealing only with minute particles. After travelling for a short distance on this current, the particles are thrown onto the aboral face of the adjacent plica;

g₂—on the aboral face of the fold, carrying dorsalward either isolated or agglutinated particles. As they proceed dorsally, they are influenced by transverse currents "c" and are removed anteriorly.

The combined action of the ciliary tracts "g₁," "g₂," and "c" causes the particles to travel in a zigzag trajectory. This is an efficient mechanism to keep the food material away from the rejection currents, allowing the agglomerations to be disintegrated, re-sorted, and useful material ingested prior to its being discarded as pseudofeces.

The mouth. Particles arriving at the proximal oral groove of *Semele purpurascens* and *S. proficua* (Figure 9) can go directly into the mouth (mo). Ciliary currents on the edges

of the lips return unwanted material to the rejection current "d," on the ventral margin of the palps.

Ciliary currents on the mantle. The ciliary currents on the inner surface of the mantle (Figure 7) converge particles into a powerful rejection tract situated parallel and close to the pallial line. The rejection tract is located in a deep groove (rg) lined with cilia longer than those present over the rest of the mantle surface. In *Semele purpurascens*, an anterior, vigorous ciliary tract concentrates the main bulk of material travelling ventralward, whereas in *S. proficua* the particles are segregated into two vigorous tracts, the anterior one being the more active (Domaneschi, 1982). Minor ciliary cleansing currents on the inner fold of the mantle pass fine particles slowly and radially inward to join the main rejection tract. All the material to be rejected is conducted to the base of the inhalant siphon.

The Alimentary Canal

The general configuration of the digestive system of *Semele purpurascens* is similar to that of *S. proficua* (Domaneschi, 1982) (Figures 12, 13), *S. solida* (Schröder, 1915), *Scrobicularia plana* (Graham, 1934), and *S. casali* (Narchi & Domaneschi, 1977). The brief description and figure given by Boss (1972) for *S. purpurascens* are in accordance with the observations of the present study.

A flattened esophagus (o) opens into the vestibule of the stomach (st) antero-dorsally. The combined style-sac (ss) and mid-gut pass from the floor of the globular region of the stomach directly posteriorly and ventrally toward the distal limit of the visceral mass into the foot.

The mid-gut (mg) leaves the subdistal end of the style-sac, turns abruptly dorsalward and immediately transforms into a tight spiral coil. From here, it ascends almost straight for a short distance before it passes through a series of coils posterior to the style-sac and the stomach. These coils are irregular and concentrated below the level of the floor of the stomach in *Semele purpurascens*; in *S. proficua* they are more regular and, observed in a dorsal view, they are seen running initially in a counter-clockwise manner, followed by clockwise spiral coils posterior to the style-sac, and irregular loops posterior to the stomach. From the last loops, next to the roof of the stomach, the hind-gut (hg) of both species turns back on itself to enter the pericardial cavity, traverses the ventricle (v), to pass over the posterior adductor muscle, then ends at the anal papilla (ap).

The globular region of the stomach is dorso-ventrally flattened. From its right dorsal side arises an evagination associated with a digitiform appendix (ax). This appendix is separated from the roof of the stomach by a bundle of muscular fibers (tm) running from one lateral wall of the visceral mass to the other. Yonge (1949) described the similar muscle attached to both shell valves in *Tellina tenuis* da Costa, 1778, and considered it a "thin adductor muscle."

From the left side of the roof of the stomach there projects

a well-developed, conical-shaped, dorsal hood (dh). Below this lies a broad, conical-shaped left pouch (lp) into which some ducts open from the digestive diverticula. The remainder of the ducts coming from the dense mass of digestive diverticula open ventrally into the stomach via right (rc) and left (lc) caeca.

The nearly straight style-sac in *Semele purpurascens* contrasts with that of *S. proficua* studied by Domaneschi (1982), which has its distal end curved, with its concavity turned posteriorly. Narchi & Domaneschi (1977) indicated that a straight style-sac exists in *S. casali*, while Schröder (1915) figured and described a widely "S"-shaped one in *S. solida*.

Stomach contents. The stomach contents of *S. purpurascens* and *Semele proficua* included amorphous organic particles, some diatoms, dinoflagellates, unidentified eggs (up to 160 μm in diameter), fragments of filamentous and sheetlike algae (some up to 500 μm wide). Mineral particles (10 μm to 450 μm in diameter) were invariably present in all examined specimens. Although constant, this material always represented the least fraction of the stomach contents; the same is true for the mid-gut contents.

Structure and Function of the Stomach

The stomachs of *Semele purpurascens* (Figure 14) and *S. proficua* are similar to each other and belong to type V as defined by Purchon (1960). The esophagus (o) has a ridged inner surface, and its orifice into the vestibule (v) of the stomach is marked by a fleshy lobed rim (rm), which arises ventrally, then ascends dorsalward to the right, and ends on the left dorsal side of the vestibule. Cilia on the lobed rim produce only vibrations but not movements of particles.

A large swelling (s) on the left wall of the vestibule separates the mouth of the dorsal hood (dh) dorsally from that of the left pouch (lp) ventrally. Isolated particles travelling dorsalward across the swollen surface "s" meet those coming from an acceptance ciliary tract at the confluence of the swelling and the fleshy lobed rim "rm," and are caught by the head of the rotating crystalline style.

The dorsal hood is a large and well-defined pocket; its posterior ventral wall is protected by a long V-shaped wing of the gastric shield (gs). A broad ridge (r), like that recorded for the psammobiids *Gari togata* Deshayes, 1854, *G. solida* and *Heterodonax bimaculatus* (Linnaeus, 1758) by Purchon (1960), Domaneschi (1992), and Narchi & Domaneschi (1993), respectively, separates the vestibule from the principal cavity of the stomach. This broad ridge arises at the median line of the anterior floor of the stomach, then passes to the right wall and, crossing the roof of the organ, enters the dorsal hood. Here, the cilia, on a series of transversely disposed ridges and grooves, carry material ventralward.

A long, narrow sorting area (sa₂) of moderately fine ridges and grooves disposed obliquely, lies along the dorsal margin of the ridge "r." Its ciliary tracts carry particles

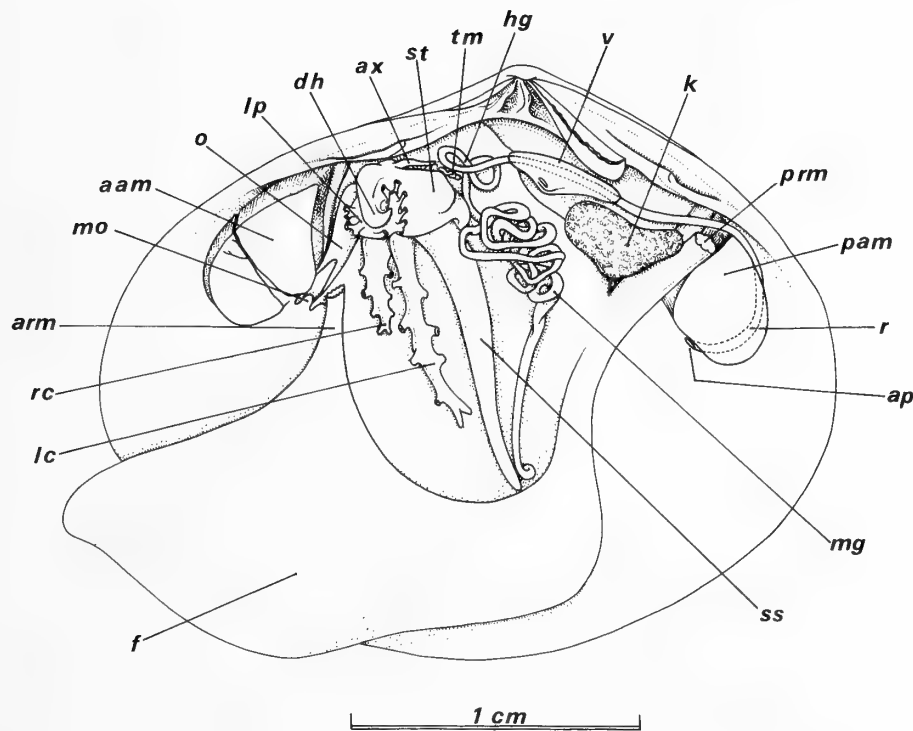


Figure 12

Semele purpurascens. Left side view of a dissected specimen showing alimentary canal. Left anterior and posterior pedal retractor muscles partially sectioned. Esophagus tangentially sectioned to expose the mouth. **ap**, anal papilla; **ax**, appendix; **dh**, dorsal hood; **hg**, hind-gut; **k**, kidney; **lc**, left caecum; **lp**, left pouch; **mg**, mid-gut; **mo**, mouth; **o**, esophagus; **r**, rectum; **rc**, right caecum; **ss**, style-sac; **st**, stomach; **tm**, transverse muscle interposed between the stomach and appendix; **v**, ventricle. For lettering (**aam**), (**arm**), (**pam**), (**prm**), see Figure 5.

deep into the distal end of the dorsal hood. On the posterior wall of this pocket lies another sorting area (**sa₅**) lined with finer ridges and grooves; cilia on it beat downward onto a ciliary tract that lies parallel to the wing of the gastric shield. Particles on this last tract are then carried out of the dorsal hood.

Sorting areas "**sa₃**" and "**sa₅**" are separated from each other by a longitudinal ridge (**r₁**) as described for the stomachs of the Mactridae and Mesodesmatidae studied by Purchon (1960). On both *Semele* analyzed here, this ridge arises near the posterior region of the aperture of the style-sac (**ss**), then extends dorsalward on the right wall of the stomach, over the roof of this organ and ends inside the dorsal hood. Its cilia carry particles toward the dorsal hood, throwing them onto "**sa₃**." The sorting area "**sa₃**" and the ridge "**r₁**" delimit a narrow ciliated groove which carries fine particles out of the dorsal hood and down into the mouth of the right caecum (**rc**).

The left pouch (**lp**) opens into the stomach antero-ventrally in relation to the mouth of the dorsal hood; its postero-dorsal wall is protected by another V-shaped wing of the gastric shield. The left pouch passes posteriorly, exceeding the dorsal hood in length and diameter, and re-

ceives about eight ducts from the digestive diverticula. Two long belts of extremely fine transversal striations (**sa₆**) line the entire surface of the walls of the left pouch not protected by the gastric shield. These two belts end just at the aperture of the left caecum. The anterior belt receives the mouth of six ducts from the digestive diverticula, into which this belt penetrates. The remaining two ducts open at the distal end of the left pouch. Cilia on "**sa₆**" beat along the ridges, moving particles centrifugally from the smooth area, splitting the two belts, and away from the mouth of the ducts of the digestive diverticula. Feeble ciliary currents on the smooth area near the mouth of the left pouch move particles onto the stomach. It was not possible to determine how the remaining material goes into the ducts of the digestive diverticula or out of the left pouch.

The gastric shield covers an extensive area of the left and posterior walls of the stomach, extending down to the mouth of the style-sac and up to the right, penetrating a dorsal evagination (**de**). Two prominent teeth exist on the shield, one dorsal to the other. They project posteriorly from their bases on the left wall of the shield, near the mouth of the dorsal hood and the left pouch. The upper surface of the dorsal tooth is continuous with the anterior

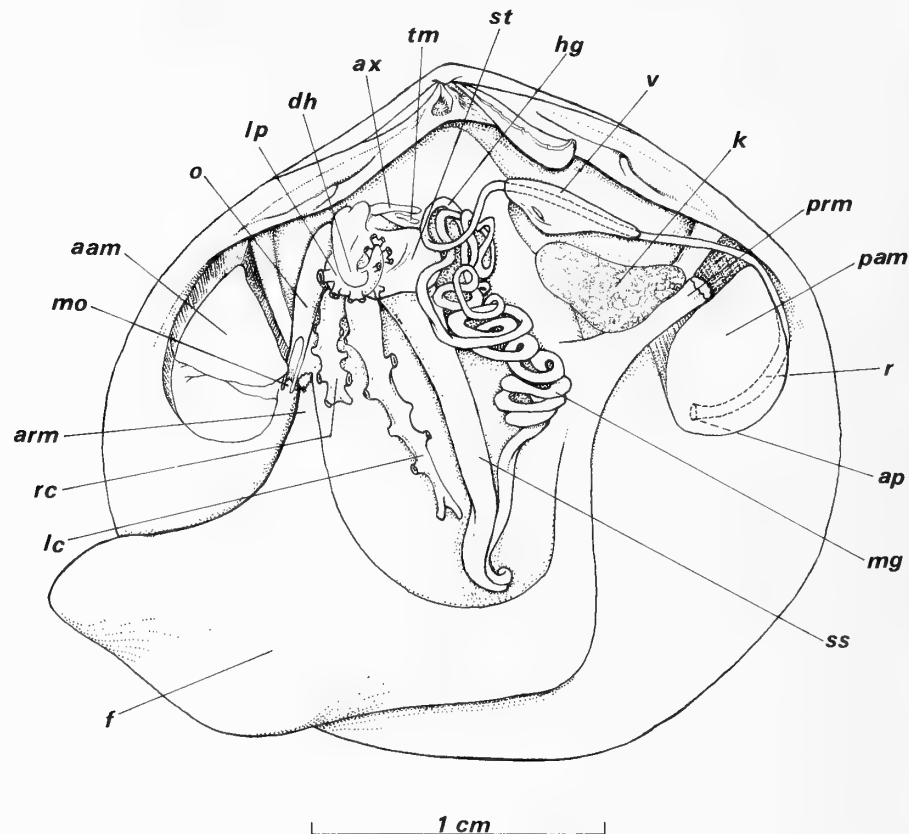


Figure 13

Semele proficua. Lettering as in Figure 12. (Redrawn after Domaneschi, 1982.)

side of the V-shaped wing which penetrates the dorsal hood.

The appendix (**ax**) is finger-shaped as in *Scrobicularia plana* (Yonge, 1949), *Donax faba* Gmelin, 1791 (Purchon, 1960), *Iphigenia brasiliensis* Lamarck, 1818 (Narchi, 1972), and *Abra tenuis* (Hughes, 1977). The appendix's opening into the stomach is situated near and behind that of the dorsal hood. The interior of this organ is finely striated. Contractions of its walls are intensive in live-dissected animals, and it was observed that the appendix shortens and enlarges more actively when its distal end is freed from its attachments. Yonge (1949) and Purchon (1960) observed similar striations and behavior in the appendix of *Tellina* and *Asaphis*, respectively. Ciliary activity is restricted to the mouth of the appendix, preventing particles from entering it.

Between the free margin of the gastric shield at the right dorsal side of the stomach and the ridge "**r**₁" lies a long triangular acceptance tract (**at**). This tract arises just at the mouth of the appendix and extends ventralward, carrying particles toward the posterior region of the mouth of the style-sac where they are caught by the rotating style.

Interposed between the ridge "**r**₁" and the intestinal

groove (**ig**) lies a long forward-projecting tongue (**el**) that nearly meets "**sa**₃" at the mouth of the dorsal hood. This sorting area (**el**) has its margin parallel to "**r**₁" bordered by a rounded smooth swelling. This swelling turns ventralward at the vicinity of "**sa**₃" toward the mouth of the right caecum and isolates, along with the ridge "**r**₁," a short ciliated groove (**ag**). Particles traveling dorsalward within the ciliated groove protected by "**r**₁" and the dorsal swelling of "**el**" either find their way into the dorsal hood or are redirected toward the right caecum via "**ag**." The sorting area "**el**" is transversely corrugated in freshly dissected stomachs; cilia on its surface either carry particles into the intestinal groove or throw them onto the major typhlosole (**ty**).

The posteroventral border of the forward projecting tongue "**el**" of *Semele purpurascens* and *S. proficua* lacks shallow blind pockets like those recorded by Purchon (1960) and Narchi (1972) for *Gari togata* and *Iphigenia brasiliensis*, respectively.

The minor typhlosole (**mt**) terminates at the mouth of the mid-gut from which it sends posteriorly a short and lobed projection around the mouth of the style-sac, sheltering a short secondary intestinal groove (**sig**). A similar

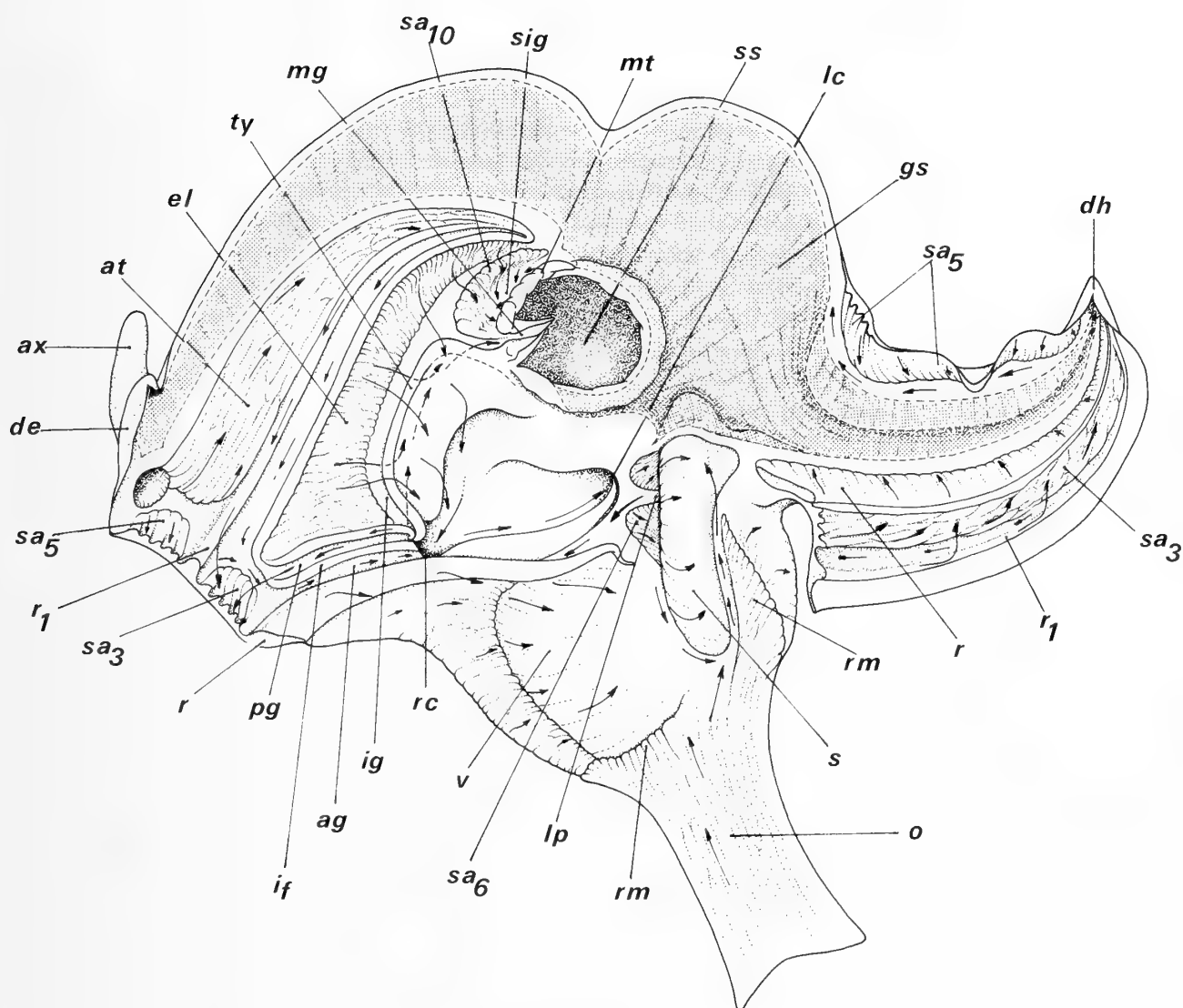


Figure 14

Semele purpurascens. The interior of the stomach seen after being opened by an incision along the dorsal wall. **ag**, anterior groove; **at**, acceptance tract; **ax**, appendix; **de**, dorsal evagination; **dh**, dorsal hood; **el**, forward projecting elevation; **gs**, gastric shield; **if**, intermediate fold; **ig**, intestinal groove; **lc**, left caecum; **lp**, left pouch; **mg**, mid-gut; **mt**, minor typhlosole; **o**, esophagus; **pg**, posterior groove; **r**, ridge passing from the anterior floor of the stomach to the interior of the dorsal hood; **rc**, right caecum; **rm**, lobed rim; **r₁**, ridge passing from the mouth of the style-sac to the interior of the dorsal hood; **s**, swelling on the left wall of the vestibule; **sig**, secondary intestinal groove; **ss**, style-sac; **sa₃** and **sa₅**, sorting areas of the dorsal hood; **sa₆**, sorting area of the left pouch; **sa₁₀**, sorting area near the mouth of the mid-gut; **ty**, major typhlosole; **v**, vestibule.

projection was illustrated by Graham (1949) and Purchon (1960) for *Solecirtus chamasolen* (da Costa, 1778) and for the clavagellacean *Brechites penis* (Linnaeus, 1758), respectively. Between the minor typhlosole and the posterior end of "el" lies a small sorting area (**sa₁₀**) with conspicuous folds that project inward toward the secondary intestinal groove into which particles are directed by ciliary action. These folds expand and contract in live animals, varying the general aspect of "sa₁₀," even in the same specimen.

In the mouth of the mid-gut (**mg**), the major typhlosole shows an unusual break in its structure, similar to that registered by Purchon (1960) for *Mya arenaria* Linnaeus, 1758 (Myacea): a short triangular flaplike portion passes down into the proximal region of the style-sac, while a separate major typhlosole arises and passes forward over the floor of the stomach, accompanied throughout its course in the usual manner by the intestinal groove. These two structures penetrate deep into the right caecum where the

typhlosole emits a tongue-shaped projection into each primary and into some of the secondary ducts of the digestive diverticula. It was difficult to determine the exact number of primary ducts opening into the right caecum, since these are complex and subdivide soon after leaving the caecum. Thus, secondary ducts receiving flares from the typhlosole are very much like the primary ones. Nevertheless, it is estimated that about eight ducts from the digestive diverticula open into the right caecum in *Semele purpurascens* and *S. proficua*.

The major typhlosole passes out of the right caecum, then transversely across the anterior floor of the stomach to enter the left caecum (**lc**), which receives nine primary ducts from the digestive diverticula in *Semele purpurascens*; Domaneschi (1982) referred to eight in *S. proficua*. The major typhlosole forms an elongated U-shaped loop within the left caecum. This segment emits a tongue-like projection into each primary duct opening and finally terminates within the caecum describing a loose spiral with $1\frac{1}{2}$ to 2 turns in *S. purpurascens* and, according to Domaneschi (1982), of $1\frac{1}{2}$ to 3 turns in *S. proficua*.

The main differences in the internal anatomy of the stomach of *Semele purpurascens* and *S. proficua* are in the anteriormost region of "**el**." In *S. purpurascens*, this region has an acute outline with an additional (intermediate) fold (**if**) isolating the anterior ciliated groove (**ag**) from a posterior one (**pg**). According to Domaneschi (1982, fig. 16), *S. proficua* has the anteriormost region of "**el**" with a rounded outline and the posterior groove absent. In this latter species, ciliary activity on the anterior region of "**el**" throws particles onto "**sa₃**," therefore, in an opposite direction to that observed in the remainder region of "**el**." A similar activity is carried out by cilia within the posterior groove (**pg**) of *S. purpurascens*, which catch particles near the mouth of the right caecum and carry them onto "**sa₃**." Despite these minor anatomical differences between the stomachs of *S. purpurascens* and *S. proficua*, the final results of the ciliary activity in the anteriormost region of "**el**" are the same in both species.

DISCUSSION

Semele purpurascens and *S. proficua* normally inhabit sand, sandy mud, and grassy, sandy mud substrata in quiet shallow waters. Nevertheless, *S. purpurascens* has been taken alive at 630 m depth off Pernambuco, Brazil, and *S. proficua* at 75 m depth (Rios, 1985), showing that it is adapted to available niches in the intertidal and infralittoral zones. From behavior in aquaria and the presence of obstacles such as pebbles and roots of sea grass in the natural habitat of the species, these semelids seem to be largely sedentary. Living in quiet waters, they are rarely scoured from the sediment.

Based on shell characters and habitat, Coan (1988) recognized two possibly polyphyletic subgenera: *Amphidesma* Lamarck, 1818, and *Semele* Schumacher, 1817, with *Amphidesma* "in general occurring farther offshore than spe-

cies of *Semele* s.s." *Semele purpurascens*, an *Amphidesma* sensu Coan (1988), has been found in the intertidal zone of the São Paulo State littoral, only near the low tide mark of extreme neap tides, corroborating Coan's observation.

The asymmetry that evolves on the posterior end of the shell of *Semele purpurascens* and *S. proficua* as the animals grow older is intimately associated with the habit of these species of lying on their left side when buried in the substratum. In this condition, the fully protruded siphons must bend to the right side to get out of the substratum. At the curved basal region of the organs, the siphonal walls maintain a regular convexity on the right (uppermost) side and a slight compression on the left. The posterior margin of the mantle lobes runs closely near the lateral walls of the siphons, taking its exact configuration. Newly deposited shell layers are molded following the configuration of the mantle edges, giving rise to the above mentioned asymmetry. Holme (1961) attributed the presence of a similar curvature to either the right or left side, in the shells of some Tellinidae he studied, to the habit of lying on either its left or right valve.

The very long, narrow, and extensive inhalant siphons of *Semele purpurascens* and *S. proficua* are anatomically similar to those described by Yonge (1949) for the deposit-feeders *Abra* and *Scrobicularia*. Nevertheless, they were never observed to bend onto or along the bottom surface sucking in deposited material; rather, the aperture is often kept free from the bottom surface or sometimes a little above or below it, drawing mostly suspended material into the pallial cavity. This behavior of the inhalant siphons is much like that recorded for the Donacidae studied by Yonge (1949), Purchon (1963), and Narchi (1972) and for the Tellinidae studied by Pohlo (1973). The lack of a waste canal in these two *Semele* species, despite their long and narrow inhalant siphon, suggests a less concentrated inhalant current, which is more compatible with a suspension feeding habit.

The general muscular systems of *Semele purpurascens* and *S. proficua* are very similar to each other and to those of *Scrobicularia plana* and *Semele solida*, described by Graham (1934) and Schröder (1915), respectively.

The intrinsic musculature of the siphonal walls of *Semele purpurascens* and *S. proficua* is structured in layers, as it is in the Tellinacea studied by Rawitz (1892, cited by Yonge, 1949), Graham (1934), Yonge (1949), and Chapman & Newell (1956). Yonge (1949) drew attention to the absence of a middle layer of circular muscle (**C₂**, in his figure 13) between the two major longitudinal layers (named by him **L₁** and **L₂**) in the Semelidae and the Tellinidae with its presence only in the Donacidae and the Asaphidae (= Psammobiidae). An equivalent middle circular layer occurs in *S. purpurascens* and *S. proficua* (Figure 5, **C₃**), showing that this is not an exclusive characteristic of the Donacidae and the Asaphidae. Yonge's (1949) statement about the Semelidae was based on *Scrobicularia plana*, considered by him to be a representative of this family. Newell (1965), Keen (1969), Hughes (1969), and Pohlo

(1982) recognized the family Scrobiculariidae, which includes only the genus *Scrobicularia* (Keen, 1969).

The activity of the siphons of *Semele purpurascens* and *S. proficua* involves changes both in length and diameter accomplished by movement of their intrinsic muscles and by the forcing of blood into the blood spaces. Retraction of these organs involves the longitudinal muscles which emerge from the base of the siphons and act as the siphonal retractors. These last muscles are characteristically composed of a number of small fan-shaped bundles of fibers. The total number of these bundles, their origin, the relative position to each other, and to what extent they contribute to the general organization of the main fan-shaped siphonal retractor of a tellinacean is presented here, for the first time, in a diagrammatical and comprehensive way. This allows one to visualize to what extent each siphon is anchored to the shell valves, and to foresee movements resulting from the nervous stimulation upon a given bundle. A similar organization of the siphonal retractors was referred to in the Donacidae, the Solecurtidae, and the Psammobiidae studied by Mouëza & Frenkiel (1974), Villarroel & Stuardo (1977), and Domaneschi (1992), respectively.

In his classic paper about the Tellinacea, Yonge (1949) did not discuss the structure of the siphonal retractors. Nevertheless, his figure 15, illustrating these muscles in *Donax vittatus* (da Costa, 1778) and *Scrobicularia plana*, shows fibers and bundles coming from one siphon criss-crossing with those coming from the other siphon. Since such an organization of the siphonal retractors is a common feature for the Donacidae, Solecurtidae, Psammobiidae, and Semelidae, it might be true for the Tellinidae as well, about which little is known. To check such a hypothesis, the author of the present study dissected *Tellina lineata* Turton, 1819, from the Brazilian littoral and proved this suspicion to be true.

Semele purpurascens and *Semele proficua* possess vestigial pedal elevator muscles. The small number and the shortness of their fibers make them functionally inoperative compared with the well-developed pedal elevator muscles present in the fast-burrowing Donacidae studied by Graham (1934), Yonge (1949), Wade (1969), and Narchi (1972, 1978). Well-developed pedal elevators were considered by Yonge (1949) to be an adaptation to life in wave-swept sandy beaches. Nevertheless, functional elevators do occur in the solecurtids *Tagelus dombeii* (Lamarck, 1818) and *T. longisinuatus* Pilsbry & Lowe, 1932, "with the same characteristics of that described by Graham (1934) in *Donax vittatus*" (Villarroel & Stuardo, 1977). Species of the Solecurtidae are normally inhabitants of either sandy or muddy substrata in quiet waters. Pedal elevator muscles are not universal among the Solecurtidae, as Graham (1934) did not find them in the species of *Solecurtus* he studied.

According to Schröder (1915), pedal elevator muscles occur in *Semele solida*. A report (Narchi & Domaneschi, 1977) indicating the absence of pedal elevator muscles in

S. casali must be revised; a later re-examination with a careful search for this, in the same specimens examined by those authors, revealed the existence of poorly developed pedal elevator muscles and the respective scars on the hinge plate. Boss (1972) seems to contest Schröder's (1915) report, since the former author, not detecting it in *S. purpurascens*, concluded that "a pedal elevator muscle does not appear to be present in *Semele*."

The presence of pedal elevator muscles in *Semele purpurascens* and *S. proficua* can easily be overlooked in living and in preserved specimens removed from the shell. Nevertheless, the well-impressed scar on the shell valves announces its presence, and also marks its location in the soft parts.

The presence of pedal elevator muscles in tellinaceans other than the Donacidae and Solecurtidae has been a matter of controversy. Pelseeneer (1911) mentioned them for *Gari*; Bloomer (1911) described and depicted those muscles for *Psammobia tellinella* [= *Gari tellinella* (Lamarck, 1818)] and *Psammobia vespertina* [= *G. depressa* (Pennant, 1777)]. Nevertheless, Graham (1934) stated that he was unable to find anything corresponding to that in *G. tellinella*, and Yonge (1949) confirmed: "there is no elevator pedal muscle in *G. tellinella*." Such controversy must partially be attributed to the difficulties in seeing this vestigial muscle.

Domaneschi (1992) described and illustrated atrophied pedal elevator muscles in the Chilean *Gari solida* (Gray, 1828) and referred to them as "very short but conspicuous muscles" inserted under the hinge plate at the same position as illustrated by Bloomer (1911) for *G. tellinella* and *G. depressa*. Pelseeneer's (1911) statement is supported by the presence of such a conspicuous muscle in *G. solida*. Evidence of pedal elevator muscles from this study of *Semele purpurascens*, *Semele proficua*, as well as from the study of *S. casali* by Narchi & Domaneschi (1977), gives support to Schröder's (1915) statement about *S. decisa*, and corroborates its presence in the genus *Semele*. Vestigial pedal elevator muscles may also be present in *S. rubropicta*, *S. incongrua*, and *S. pulchra*, because in their respective shell figures, Coan (1973) delineated a scar at the same position where the pedal elevator muscle scar of *S. purpurascens* and *S. proficua* is found. Unfortunately, Coan (1973) did not refer to the scar in the text or identify it in his figures and respective legends.

Based on the habits and general structure of all available British species of the Tellinacea, Yonge (1949) offered several statements emphasizing the habit of deposit-feeding as universal within this group. Some passages in the same paper, however, show that the feeding pattern among the Tellinacea may not be so restricted. Subsequent studies have shown that the group embraces a full spectrum of feeding habits with a gradation from deposit to suspension feeding (Pohlo, 1969). This statement was revised by Pohlo (1982). This confusion concerning the nature of feeding in the Tellinacea received exhaustive consideration by Pohlo (1969, 1982), Reid & Reid (1969), and Reid (1971).

Semele purpurascens and *S. proficua* have a mosaic of morphological features, some typical of specialized deposit-feeders, others of the suspension-feeding tellinaceans. Typical of the deposit-feeding tellinaceans, in both species there is a long and narrow inhalant siphon, as long as 4 times the shell length, provided with non-straining tentacles; there is an upturned outer demibranch [type E(a) of Atkins (1937b)], which has one feeding-respiratory surface lost; there is also the habit of lying on one side while under the substratum.

Features of *Semele purpurascens* and *S. proficua* which relate to a suspension feeding habit include large ctenidia relative to the labial palps which are not hypertrophied; plicate demibranchs (except the outer ones in *S. purpurascens*), with the inner one containing a well-developed marginal food groove protected by fan-shaped groups of guard-cilia; the lack of a waste canal and lack of horizontal mobility while burrowed in the substratum. In addition, the passive behavior of the inhalant siphon, which exposes a trumpet-shaped aperture well clear of the bottom surface, along with the reduced amount of mineral grains in the stomach and midgut content, seem to confirm the suspension feeding habit of *S. purpurascens* and *S. proficua*.

Despite the preponderance of fine, suspended particles in the stomach contents, both species may derive part of their nutritional requirements from loose surface deposits as well as from dense deposited material. Benthic organisms and sand grains fall passively into the pallial cavity when the inhalant aperture is kept widely open, or slightly below or at the sediment surface. This may allow deposited material to ultimately reach the stomach.

Atkins (1937b) stated that the Semelidae lack a true marginal food groove; its absence was associated by Yonge (1949) with the need to reduce as much as possible the volume of material carried forward in the deposit-feeding Tellinacea which deal with large amounts of material.

In their study of *Semele casali*, Narchi & Domaneschi (1977) reported, for the first time, a true marginal food groove in the Semelidae. The well-developed marginal food groove present in both *Semele* species here studied has mobile lateral walls, which move toward and away from one another, acting as a sorting mechanism. The tips of the opposite fan-shaped groups of guard-cilia touching each other create an efficient barrier against the entrance of unwanted material. This mechanism also prevents selected material moving oralward inside the food groove to be lost, unless in the anterior region where it will be passed to the sorting mechanisms on the palps. If the surrounding water is scanty in food material, the walls of the food groove and their respective guard-cilia may move away, the latter permitting, then, the admittance of unusual large particles; submitted to a turbid water, this same mechanism permits the rejection of the excess of material travelling oralward inside the marginal food groove.

Such a specialized sorting device, associated with the presence of an active oralward current along the ctenidial

axis, is further evidence that *Semele purpurascens* and *S. proficua* do not introduce large amounts of material into the pallial cavity, as do typical deposit-feeders, and that these species feed largely by filtering suspended particles. Boss (1972) probably had no opportunity to observe oralward current on the ctenidial axis of *S. purpurascens* and generalized: "there is no forward-running current along the gill axis of *Semele*." A marginal food groove, acting as a sorting mechanism as in *S. purpurascens* and *S. proficua*, was noted by Purchon (1963) for the donacid *Egeria radiata*, which "feeds solely by filtration of the river water."

According to Atkins (1937a), guard-cilia are presumably efficient in dealing with the particles of muddy soil, but are not sufficiently robust when coarse material has to be dealt with. Living in sand and sandy mud substrata, *Semele purpurascens* and *S. proficua* have to deal, although sporadically, with both types of material. Although they lack the large frontal cilia to which Atkins (1937a) and Narchi & Domaneschi (1993) attributed the function of removing unwanted material such as sand grains from the ctenidia, other structures counterbalance its absence: the pallial cleansing mechanisms, the guard-cilia, and the sorting device on the palps create an efficient barrier against an excess of mineral particles travelling oralward. The palps are responsible for the main selection before material is passed to the mouth, concurring with the low frequency of mineral grains in the stomach.

The possession of a mosaic of morphological and ecological features typical of both suspension and deposit-feeders, as observed in *Semele purpurascens* and *S. proficua*, was considered by Pohlo (1982) as an intermediate step in the evolution of the Tellinacea; this proceeded from a selective suspension-feeding ancestor (modern *Donax* species may be representative of this primitive condition) to the modern and exclusively deposit-feeders numerous today in the Tellinidae, Scrobiculariidae (this recognized as a distinct family by Pohlo, 1982), and in some of the Semelidae.

ACKNOWLEDGMENTS

I would like to thank Dr. Walter Narchi, Instituto de Biociências, Universidade de São Paulo, and M. Sc. Fábio Moretzsohn for their valuable suggestions which improved the manuscript, and Conselho Nacional de Desenvolvimento Científico e Tecnológico-CNPq (Brasília, Brazil) for financial support during elaboration of this paper.

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New Freshwater Snails of the Genus *Pyrgulopsis* (Rissooidea: Hydrobiidae) from California

by

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Abstract. Seven new species of Recent springsnails belonging to the large genus *Pyrgulopsis* are described from California. *Pyrgulopsis diablensis* sp. nov., known from a single site in the San Joaquin Valley, *P. longae* sp. nov., known from a single site in the Great Basin (Lahontan system), and *P. taylori* sp. nov., narrowly endemic in one south-central coastal drainage, are related to a group of previously known western species also having terminal and penial glands on the penis. *Pyrgulopsis eremica* sp. nov., from the Great Basin and other interior drainages in northeast California, and *P. greggi* sp. nov., narrowly endemic in the Upper Kern River basin, differ from all other described congeners in lacking penial glands, and are considered to be derived from a group of western species having a small distal lobe and weakly developed terminal gland. *Pyrgulopsis gibba* sp. nov., known from a few sites in extreme northeastern California (Great Basin), has a unique complement of penial ornament consisting of terminal gland, Dg3, and ventral gland. *Pyrgulopsis ventricosa* sp. nov., narrowly endemic in the Clear Lake basin, is related to two previously described California species also having a full complement of glands on the penis (Pg, Tg, Dg1-3) and an enlarged bursa copulatrix.

INTRODUCTION

The author recently reviewed the taxa belonging to *Pyrgulopsis* Call & Pilsbry, 1886, the second largest genus (65 Recent species) of freshwater gastropods in North America (Hershler, 1994). The focus of that paper was on previously described forms, although it was recognized that perhaps an equal number of undescribed species await attention in the western United States. While such novelties abound throughout many of the western states, California, which has only 10-11 currently recognized species (one may now be extinct in the state), may harbor an especially large group, given that this huge state is well-watered and has an extremely complex hydrographic history owing to tectonism and associated climatic factors (Minckley et al., 1986). Published taxonomic studies on hydrobiid snails and other small freshwater gastropods from California are few (Taylor, 1981), and collecting efforts have been largely concentrated in only four regions: Great Basin and Klamath system to the northeast, lower Sacramento system in the San Francisco environs, Death Valley region, and south-coastal and Salton Sea drainage to the southwest. Of these, only the Death Valley region hydrobiids have been thoroughly surveyed and documented

in the literature (Hershler & Sada, 1987; Hershler, 1989; Hershler & Pratt, 1990).

To gain a better understanding of the California *Pyrgulopsis*, the author recently collected material of this genus from various parts of the state. Represented among these collections were seven new species, which are described below. While these species are discussed within the context of the preliminary phylogenetic hypothesis proposed for the genus by Hershler (1994), a revised analysis incorporating these new data is deferred pending description of the many other new species known from the West.

MATERIALS AND METHODS

Institutional acronyms are USNM (National Museum of Natural History, Smithsonian Institution), and WBM (personal collection of Walter B. Miller, now housed [uncatalogued] at Santa Barbara Museum of Natural History). Anatomical study was of alcohol-preserved snails that had been relaxed with menthol crystals and fixed in dilute (about 4%) formalin. Methods of anatomical study, terminology, and characters are those of Hershler (1994). Anatomical illustrations were prepared from camera lu-

Table 1

Shell parameters for new species of *Pyrgulopsis*. μ = mean, s = standard deviation, SH = shell height, SW = shell width, HBW = height of body whorl, WBW = width of body whorl, AH = aperture height, AW = aperture width, W = whorl expansion rate, D = distance of generating curve from coiling axis, T = translation rate, AS = aperture shape. Measurements are in mm.

		WH	SH	SW	HBW	WBW	AH	AW	W	D	T	AS
<i>P. diablensis</i>												
USNM 883791	μ	4.90	3.76	2.36	2.73	2.07	1.70	1.28	1.80	0.54	5.64	1.34
n = 17	s	0.22	0.30	0.22	0.18	0.12	0.11	0.09	0.15	0.07	1.14	0.07
<i>P. eremica</i>												
USNM 858264	μ	4.03	1.90	1.28	1.42	1.15	0.82	0.68	2.28	0.56	5.29	1.20
n = 15	s	0.13	0.16	0.11	0.12	0.09	0.82	0.05	0.32	0.05	0.64	0.06
USNM 858265	μ	4.10	2.17	1.43	1.62	1.28	0.95	0.77	2.12	0.61	5.31	1.24
n = 15	s	0.16	0.18	0.09	0.11	0.07	0.07	0.04	0.26	0.04	0.92	0.06
USNM 858266	μ	4.48	2.66	1.73	1.95	1.54	1.20	0.94	2.12	0.57	5.72	1.27
n = 11	s	0.21	0.22	0.11	0.15	0.11	0.08	0.06	0.27	0.03	0.58	0.04
USNM 858267	μ	4.08	1.89	1.26	1.41	1.13	0.81	0.66	2.29	0.56	5.49	1.23
n = 12	s	0.20	0.12	0.07	0.07	0.05	0.05	0.04	0.42	0.03	0.47	0.06
USNM 858271	μ	4.18	2.67	1.99	2.12	1.70	1.33	1.03	2.43	0.55	4.09	1.30
n = 15	s	0.22	0.17	0.10	0.10	0.08	0.07	0.05	0.42	0.04	0.45	0.04
USNM 873138	μ	4.14	2.45	1.72	1.86	1.47	1.13	0.93	2.28	0.60	4.63	1.21
n = 14	s	0.16	0.15	0.11	0.11	0.08	0.09	0.06	0.23	0.04	0.32	0.05
<i>P. gibba</i>												
USNM 858275	μ	4.25	2.93	1.99	2.26	1.70	1.37	1.13	2.04	0.60	5.10	1.21
n = 10	s	0.20	0.16	0.12	0.13	0.10	0.09	0.08	0.13	0.05	0.70	0.03
USNM 858273	μ	4.33	3.34	2.28	2.54	1.94	1.60	1.30	2.09	0.58	5.02	1.24
n = 10	s	0.17	0.13	0.10	0.11	0.08	0.06	0.07	0.27	0.05	0.38	0.05
<i>P. greggi</i>												
USNM 874139	μ	4.38	2.31	1.47	1.68	1.27	0.99	0.82	2.06	0.60	5.24	1.21
n = 15	s	0.27	0.16	0.09	0.11	0.11	0.07	0.04	0.45	0.03	0.67	0.04
USNM 874140	μ	4.21	1.74	1.21	1.32	1.06	0.77	0.75	2.52	0.61	4.66	1.17
n = 13	s	0.33	0.10	0.07	0.07	0.05	0.77	0.72	0.60	0.06	0.55	0.06
<i>P. longae</i>												
USNM 858262	μ	4.23	2.76	1.79	2.03	1.53	1.24	0.97	2.30	0.57	5.25	1.30
n = 15	s	0.24	0.18	0.15	0.15	0.11	0.10	0.06	0.39	0.05	0.94	0.05
<i>P. taylora</i>												
USNM 883792	μ	4.63	2.28	1.28	1.59	1.11	1.05	0.73	1.71	0.56	6.00	1.44
n = 17	s	0.37	0.19	0.12	0.13	0.08	0.07	0.07	0.14	0.07	1.25	0.08
USNM 883789	μ	4.63	2.80	1.67	2.03	1.41	1.30	0.90	1.85	0.54	5.00	1.46
n = 16	s	0.37	0.24	0.15	0.13	0.10	0.10	0.09	0.18	0.05	0.84	0.10
<i>P. ventricosa</i>												
USNM 883790	μ	4.14	2.37	1.66	1.83	1.45	1.18	0.91	2.31	0.59	5.04	1.29
n = 16	s	0.16	0.12	0.12	0.10	0.09	0.09	0.04	0.38	0.05	0.72	0.08

cida drawings. Methods of shell measurements are those of Hershler (1989); data are presented in Table 1.

SYSTEMATICS

Family HYDROBIIDAE

Subfamily NYMPHOPHILINAE

Pyrgulopsis Call & Pilsbry, 1886

Type Species: *Pyrgula nevadensis* Stearns, 1883; original designation.

Diagnosis: The genus was recently diagnosed by Hershler (1994).

Pyrgulopsis diablensis Hershler, sp. nov.

(Figures 1–3, 5A)

Etymology: Referring to occurrence of this species in the Diablo Range of central California.

Diagnosis: Shell ovate- to narrow-conic, medium-sized, umbilicate. Penial filament medium length; lobe short.

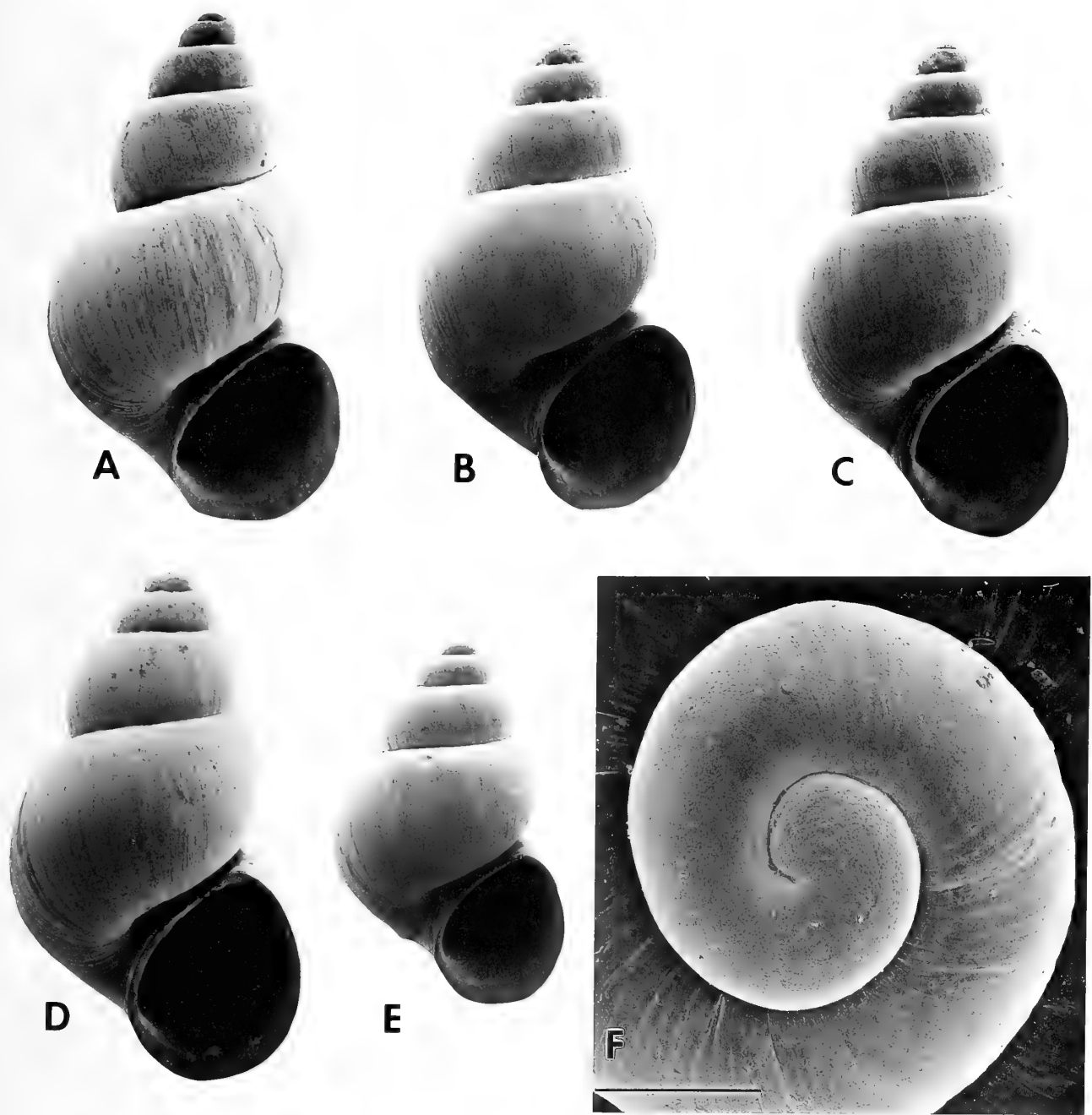


Figure 1

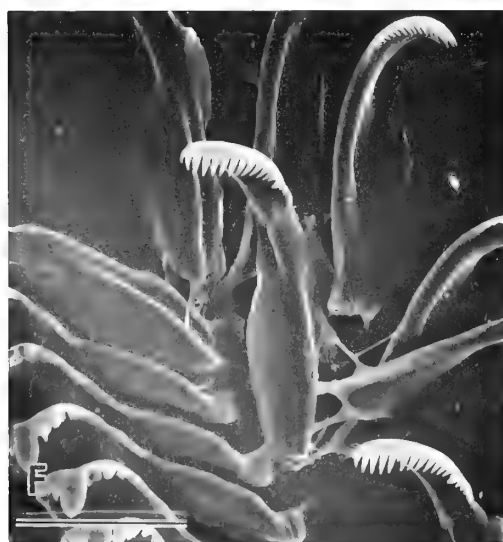
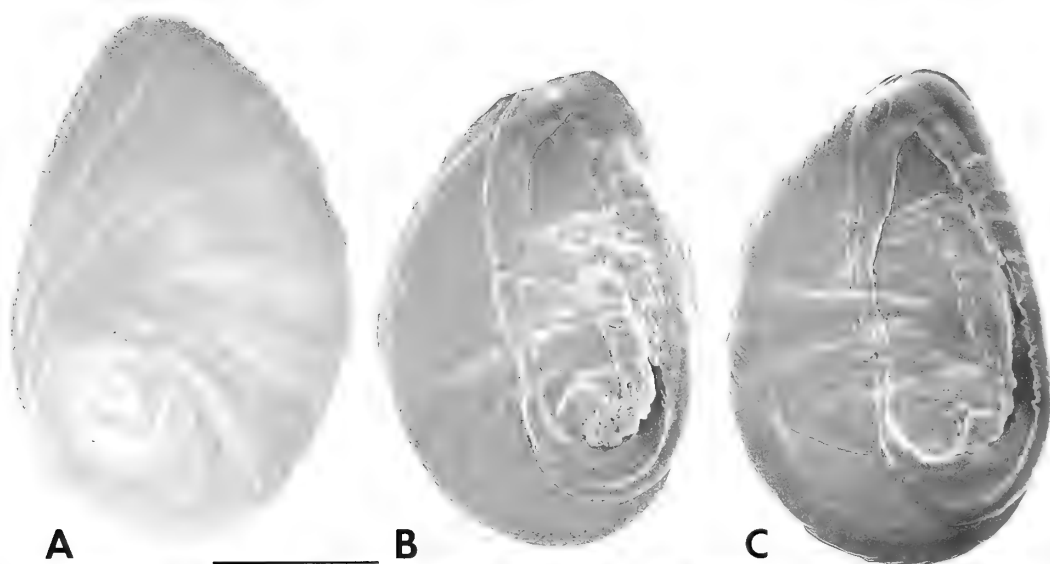
Scanning electron micrographs of shells of *P. diablensis* Hershler, sp. nov., USNM 883791. F. Protoconch, bar = 150 μ m. Shell "A" is 3.8 mm tall; other shells printed to same scale.

Penial ornament a short penial gland and small terminal gland.

Description: Shell (Figures 1, 5A) ovate- to narrow-conic; height 3.1–4.3 mm; whorls 4.25–5.0. Protoconch (Figure 1F) slightly less than 1.5 whorls, early portion strongly wrinkled. Teleoconch whorls convex, sometimes strongly shouldered; sculpture of strong growth lines. Aperture ovate,

usually slightly separated from body whorl. Inner lip complete, thin, without columellar shelf. Outer lip thin, slightly prosocline. Umbilicus rimate to perforate. Periostracum light brown.

Operculum (Figure 2A–C) ovate, amber with brown to red attachment scar region; nucleus eccentric; dorsal surface frilled. Attachment scar thickened, often strongly so, all around. Callus large, well developed.



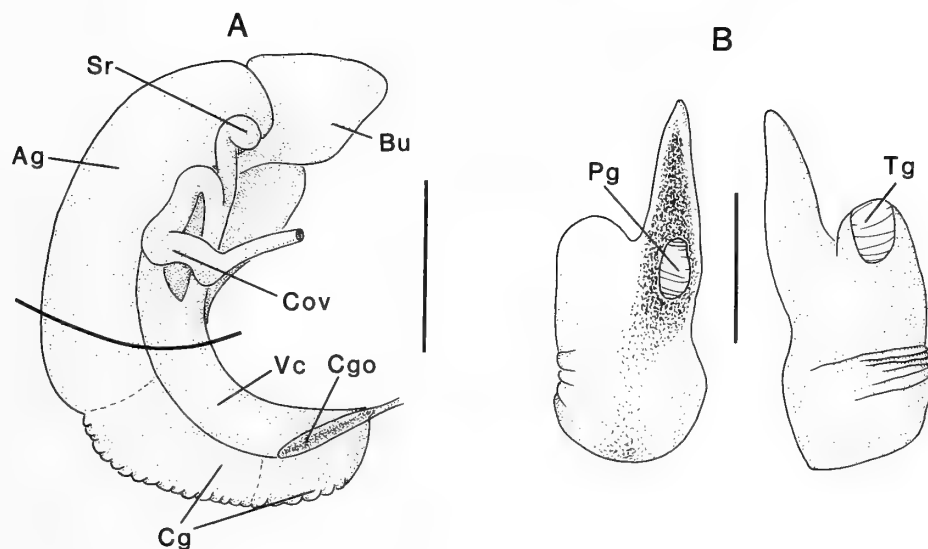


Figure 3

Genital morphology of *P. diablensis* Hershler, sp. nov., USNM 883791. A. Distal female genitalia (left side). Bar = 0.5 mm. B. Penis (dorsal aspect, left; ventral aspect, right). Bar = 0.5 mm. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Pg = penial gland, Sr = seminal receptacle, Tg = terminal gland, Vc = ventral channel.

Buccal mass large; radular sac protruding behind buccal mass as short coil. Radula ribbon elongate, about 0.89×0.11 mm, with about 60 rows of teeth. Central radular tooth (Figure 2D) trapezoidal, with medium to highly indented dorsal edge; lateral cusps 4–5; central cusp slightly pointed, considerably broader and longer than laterals; basal cusps 1, medium-sized, with medium dorsal support. Basal process medium width; basal sockets deep. Lateral margins slightly thickened, with weakly developed neck. Lateral tooth (Figure 2E) formula 3-1-3(4); neck weakly developed; basal tongue well developed; outer wing about 140% of cutting edge length. Marginal teeth (Figure 2F, G) with about 15–19 (inner) and 16–23 (outer) cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles pale, but with light grey internal pigment proximally. Snout, foot grey to black. Opercular lobe black along inner edge, sides; outer edge pale to black. Neck pale to grey. Pallial roof black, somewhat lighter on pallial gonoducts. Visceral coil black.

Ctenidial filaments 25, medium height, width; ctenidium ending slightly anterior to pericardium. Osphradium medium-sized, centered slightly posterior to middle of cten-

idial axis. Kidney with medium pallial bulge; renal gland longitudinal-slightly oblique; kidney opening white. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland medium thickness; overlapping rectum, pallial gonoducts, narrow section of posterior pallial roof adjacent to rectum.

Distal female genitalia shown in Figure 3A. Ovary 1.5 whorls, slightly overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland considerably shorter than albumen gland. Genital aperture a broad slit, with short vestibule. Coiled oviduct circular-oblique, kinked at mid-point, augmented by proximal twist or small coil. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix broadly ovate-triangular, about one-fourth length of albumen gland, and about two-thirds width of gland, with three-fourths or more of length posterior to gland. Bursa duct narrow-medium width, about 150% of length of bursa copulatrix, shallowly embedded in albumen gland. Seminal receptacle a broad, folded pouch, about 50% of length of bursa copulatrix, usually overlapping proximal bursa duct. Seminal receptacle duct medium length.

Testis 2.0 whorls, overlapping stomach to posterior edge

Figure 2

Scanning electron micrographs of opercula and radula of *P. diablensis* Hershler, sp. nov., USNM 883791. A–C. Opercula; bars = 0.43 mm. D. Central radular teeth, bar = 15 μ m. E. Lateral teeth, bar = 20 μ m. F. Inner marginal teeth, bar = 30 μ m. G. Outer marginal teeth, bar = 20 μ m.



of style sac. Prostate gland fat bean-shape; oval in cross section; pallial section short. Pallial vas deferens with strong proximal twist. Penis (Figure 3B) large; base broadly rectangular, edges with several weak folds proximally; filament about two-thirds length of base, medium width, gently tapering, parallel or slightly oblique to long axis of base; lobe hemispherical, short. Terminal gland medium size, circular or elongate-transverse, usually restricted to ventral surface, rarely interrupted (two units). Penial gland short, medium width, restricted to base of filament. Filament darkly pigmented internally; pigment continuing weakly onto distal penis.

Type locality: Unnamed creek, Del Puerto Canyon, Del Puerto Road, 20 km west of HW 5, Stanislaus County, California, T. 6 S, R. 6 E, NE $\frac{1}{4}$ sec. 8 (Figure 4A). Holotype, USNM 860645; paratypes, USNM 883791, collected by R. Hershler, 4 May 1994. Snails were commonly found in this medium-sized (ca. 2 m wide, 0.5 m deep), poorly shaded stream, which was slightly disturbed from pastoral and recreational activities.

Remarks: The presence of a penial gland (Pg) in this species suggests affinity with a large group of western American species defined, in part, by this synapomorphy, and closely conforming to Taylor's (1987) "*californiensis* series" (see Hershler, 1994). Of the members of this group, however, only this species plus *P. longae* and *P. taylori* (both described below) lack a ventral gland (or any vestige thereof). *Pyrgulopsis diablensis* is similar to *P. longae* in configuration of the distal female genitalia (i.e., broad coiled oviduct, frequently pyriform or triangular bursa copulatrix), but differs in its more attenuate shell, stronger opercular attachment scar, stouter penis, and larger terminal gland.

This species is thus far known only from the type locality in the Diablo Range, northern San Joaquin Valley (Figure 6).

Pyrgulopsis eremica Hershler, sp. nov.

(Figures 5B, 7-9)

Fluminicola modoci [in part] Hannibal, 1912:187 (Fritter's spring, head of Willow Creek, Honey Lake basin; Troxel's spring, Eagle Lake).

Etymology: From classical Greek *eremos*, meaning solitary or lonely, and referring to occurrence of this species in the fairly remote Smoke Creek Desert and adjacent environs.

Diagnosis: Shell broad- to narrow-conic, small- to medium-sized, umbilicate. Penis a narrow blade; penial filament medium-elongate; lobe absent. Penial ornament absent.

Description: Shell (Figures 5B, 7) broad- to narrow-conic; height 1.7–3.2 mm; whorls 3.75–4.75. Protoconch (Figure 7K) about 1.5 whorls, early portion densely wrinkled and lined with scattered spiral striae. Teleoconch whorls convex, strongly shouldered; sculpture of weak growth lines and faint spiral striae. Aperture ovate, broadly adnate to slightly separated from body whorl. Inner lip complete, thin to slightly thickened, without columellar shelf. Outer lip thin, orthocline to slightly prosocline. Umbilicus narrowly rimate to deeply perforate. Periostracum tan to brown.

Operculum (Figure 8A–C) ovate, amber except for orange nuclear region; nucleus slightly eccentric; dorsal surface frilled. Attachment scar thickened all around, especially along inner edge. Callus sometimes well developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radula ribbon elongate, about 0.59×0.09 mm, with about 65 rows of teeth. Central radular tooth (Figure 8A, B) trapezoidal, with medium to highly indented dorsal edge; lateral cusps 5–6; central cusp spoonlike, slightly broader and considerably longer than laterals; basal cusps 1, medium-sized, with medium dorsal support. Basal process narrow; basal sockets deep. Lateral margins slightly thickened, with pronounced neck. Lateral tooth (Figure 8F–H) formula 3(4)–1–5; neck weakly developed; basal tongue weakly developed; outer wing about 200% of cutting edge length. Marginal teeth (Figure 8F, G, I) with about 21–23 (inner) and 23–28 (outer) cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles medium to black, sometimes pale distally. Snout medium-(more commonly) black. Foot pale to dark along sides, anterior and posterior edges usually dark. Opercular lobe broadly darkened along sides, somewhat lighter along inner edge. Neck pale to dark. Pallial roof, visceral coil black.

Figure 4

Photographs of type localities of new species of *Pyrgulopsis* from California. A. Unnamed creek, Del Puerto Canyon, Stanislaus County (*P. diablensis* Hershler, sp. nov.). B. Unnamed springs tributary to Willow Creek, Lassen County (*P. eremica* Hershler, sp. nov.). C. Unnamed springs west of Fee Reservoir, Modoc County (*P. gibba* Hershler, sp. nov.). D. Grapevine Creek, Kern County (*P. greggi* Hershler, sp. nov.). E. Unnamed spring, ca. 4.8 km west-southwest of Hallelujah Junction, Lassen County (*P. longae* Hershler, sp. nov.). F. Unnamed spring, 7.4 km south of HW 29 along Seigler Canyon Road, Lake County (*P. ventricosa* Hershler, sp. nov.). G. Unnamed spring, 4.8 km north of San Luis Obispo, east of HW 101, San Luis Obispo County (*P. taylori* Hershler, sp. nov.).

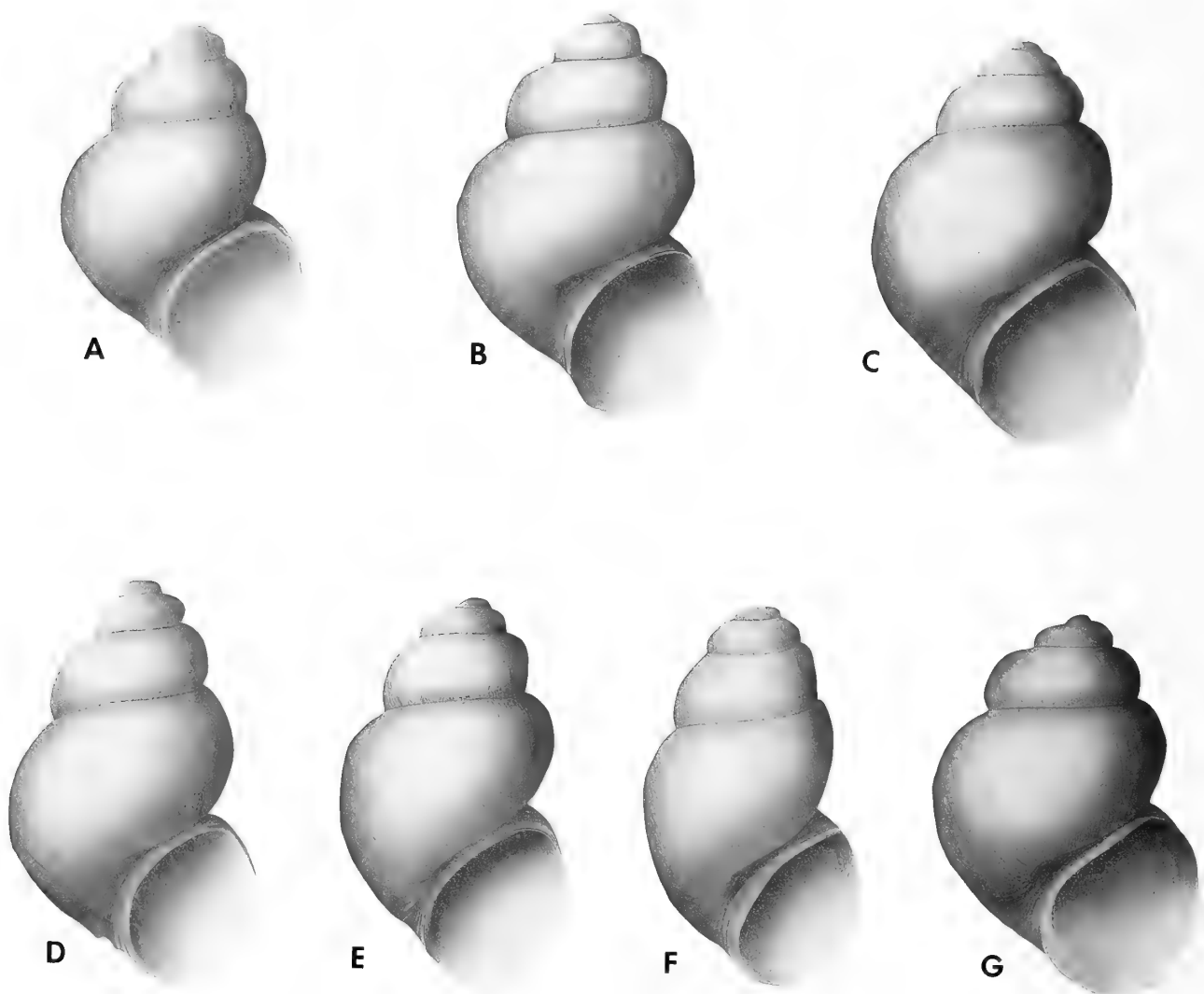


Figure 5

Shells (holotypes) of new *Pyrgulopsis* species. A. *P. diablensis* Hershler, sp. nov., USNM 860645 (3.1 mm tall). B. *P. eremica* Hershler, sp. nov., USNM 860644 (1.9 mm). C. *P. gibba* Hershler, sp. nov., USNM 860643 (3.1 mm). D. *P. greggi* Hershler, sp. nov., USNM 860641 (2.4 mm). E. *P. longae* Hershler, sp. nov., USNM 860642 (3.0 mm). F. *P. taylori* Hershler, sp. nov., USNM 860646 (2.0 mm). G. *P. ventricosa* Hershler, sp. nov., USNM 860647 (2.4 mm).

Ctenidial filaments 14, short, narrow; ctenidium ending slightly anterior to pericardium. Osphradium medium-sized, centered slightly posterior to middle of ctenidial axis. Kidney with medium pallial bulge; renal gland longitudinal; kidney opening opaque. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland thin; overlapping rectum, pallial gonoducts.

Distal female genitalia shown in Figure 9A. Ovary 0.75 whorl, overlapping posterior stomach chamber. Pallial albumen gland medium-sized. Capsule gland slightly shorter than albumen gland. Genital aperture a broad slit with short vestibule. Coiled oviduct of two oblique-circular,

broadly overlapping coils. Distal coil sometimes lightly pigmented. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix clublike, slightly less than half of length of albumen gland, narrow relative to width of albumen gland, with one-fifth to one-half of length posterior to gland. Bursa duct narrow, about as long as bursa copulatrix, slightly embedded in albumen gland. Seminal receptacle a narrow pouch, slightly less than one-half length of bursa copulatrix, overlapping anterior one-half of bursa copulatrix. Seminal receptacle duct medium length.

Testis 2.0 whorls, overlapping stomach to posterior edge of style sac. Prostate gland bean-shaped; narrow in cross

section; pallial section medium. Pallial vas deferens with proximal twist. Penis (Figure 9B) small, narrow; base rectangular, smooth along inner edge; filament slightly shorter to slightly longer than base, slightly narrower than base, gently tapering, parallel to long axis of base; lobe absent. Penial ornament absent. Virtual entirety of filament and distal base darkly pigmented internally.

Type locality: Unnamed springs tributary to Willow Creek, Willow Creek Valley, Lassen County, California, T. 32 N, R. 11 E, SE $\frac{1}{4}$ sec. 35 (Figure 4B). Holotype, USNM 860644 (Figure 5B); paratypes, USNM 858264, collected by R. Hershler and D. Sada, 4 August 1990. Snails were commonly found in watercress in this series of small, cool, relatively pristine springs draining to a small meadow alongside Willow Creek.

Remarks: This species and *P. greggi*, described below, differ from all other described members of the genus in lacking penial glands. I interpret this character state as secondarily reduced from a glandular condition, and given that these taxa conform to "typical" *Pyrgulopsis* in all other respects, place them in this genus rather than create a new higher taxon. It is likely that these species are allied to the group of western American forms having a small distal lobe and weakly developed terminal gland (described in Hershler, 1994): both the lobe and gland are extremely reduced and even sometimes absent in some members of this group (i.e., *P. bryantwalkeri* Hershler, *P. stearnsiana* [Pilsbry], and *P. thompsoni* Hershler). *Pyrgulopsis eremica* differs from *P. greggi* in its larger size, stronger basal tongue on lateral radular teeth, smaller ctenidium, larger albumen gland, and occasional pigmentation of coiled oviduct.

Both this species and *P. longae* (described below), which also occurs in the Honey Lake basin, differ from *P. melina* Taylor, 1981 (in Taylor & Smith, 1981), described from Pliocene Honey Lake fossils, by their much smaller size, more convex whorls, and weaker columellar callus.

Pyrgulopsis eremica is distributed among springs and spring groups within the Great Basin of northeast California, including a portion of the Lahontan system (Honey Lake basin, Smoke Creek Desert) and smaller basins to the north (Eagle Lake basin, Horse Lake basin; Figure

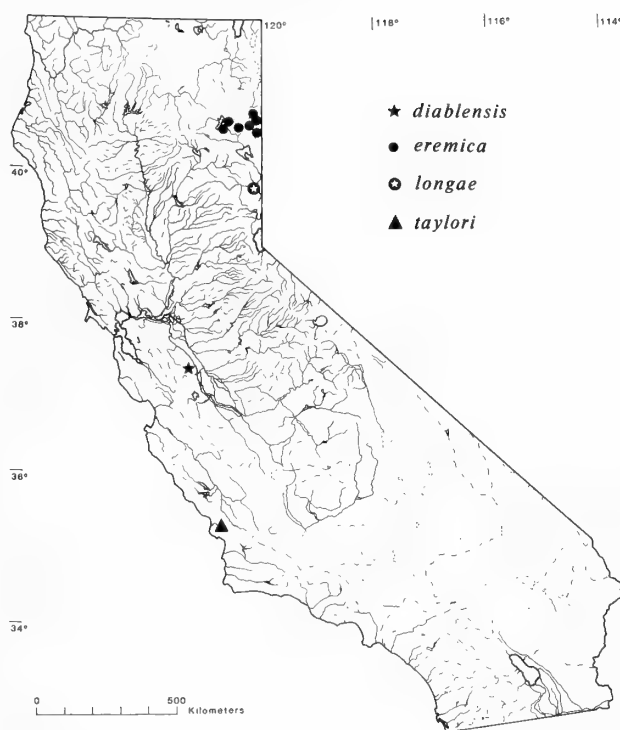


Figure 6

Map showing distributions of *P. diablensis* Hershler, sp. nov., *P. eremica* Hershler, sp. nov., *P. longae* Hershler, sp. nov., and *P. taylora* Hershler, sp. nov. Symbols may refer to more than one locality.

6). This snail probably also occurs in additional drainages within the above areas (Snowstorm Creek, northeast flank of Skedaddle Mountains, drainage west-northwest of Observation Peak, Van Loan Creek) that could not be thoroughly searched because of access problems.

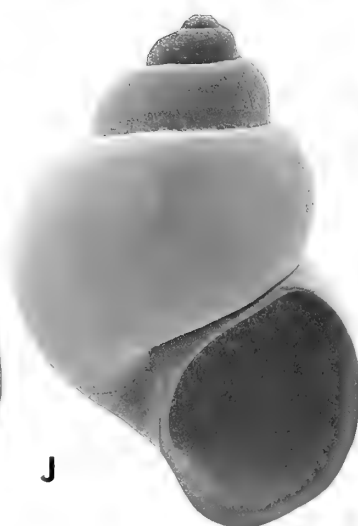
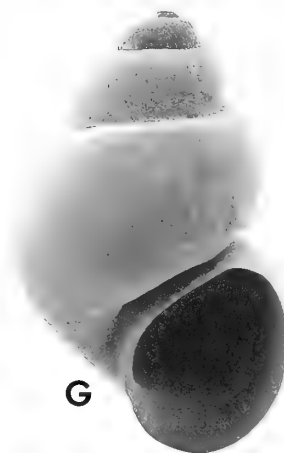
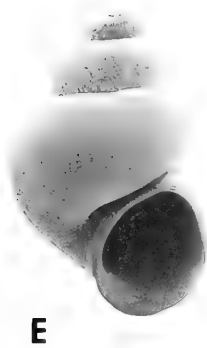
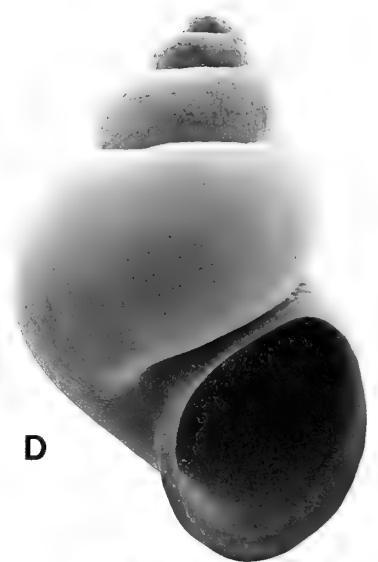
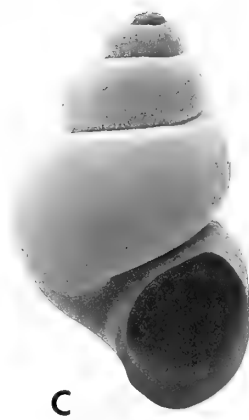
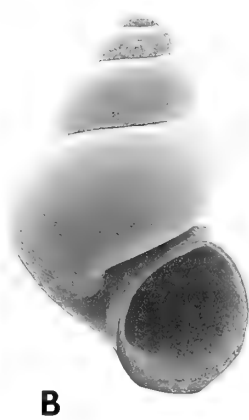
Material examined: CALIFORNIA. LASSEN COUNTY: unnamed springs, Murrers Lower Meadow, Willow Creek Valley, T. 32 N, R. 11 E, SW $\frac{1}{4}$ sec. 35, USNM 874026; unnamed spring east of Troxel Point, Eagle Lake basin, T. 32 N, R. 12 E, SW $\frac{1}{4}$ sec. 5, USNM 858265;

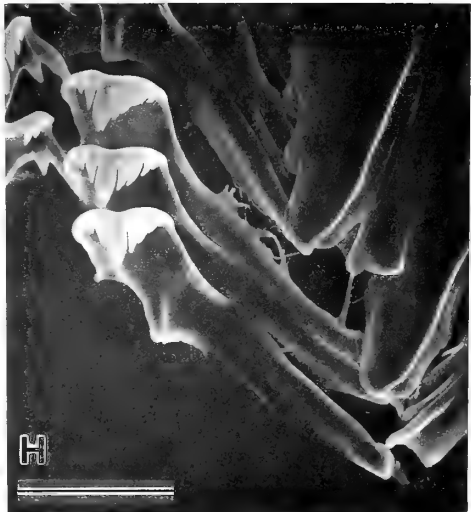
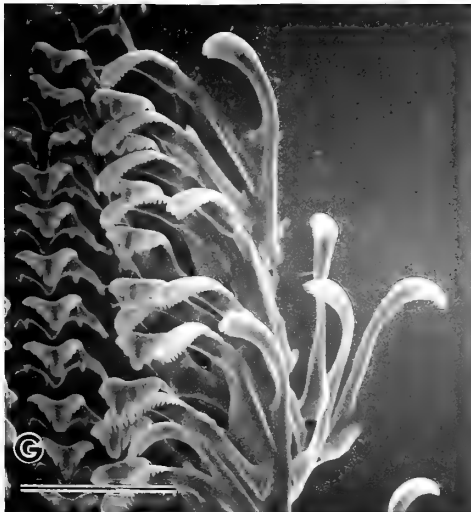
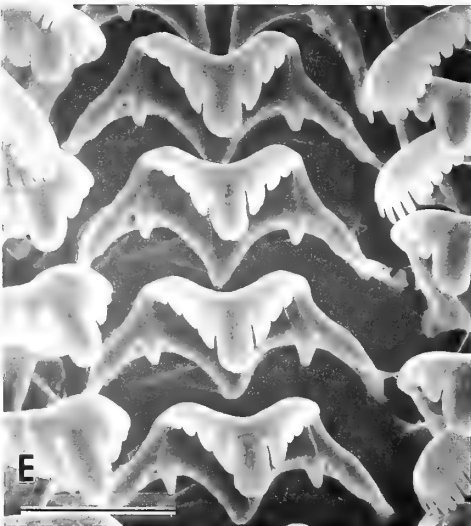
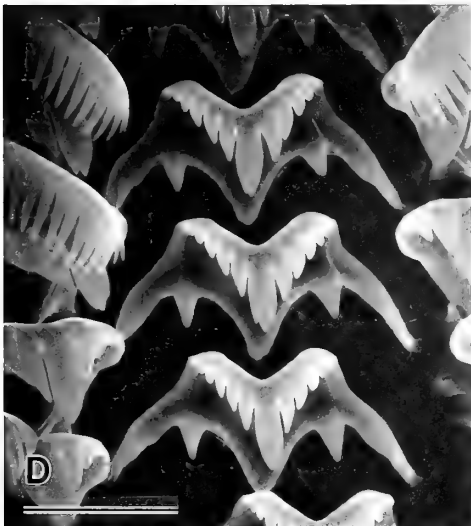
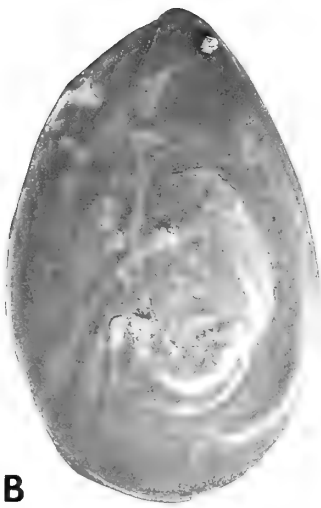
Figure 7

Scanning electron micrographs of shells of *P. eremica* Hershler, sp. nov. A–C. USNM 858264. D. USNM 858270. E, F. USNM 858267. G, H. USNM 858265. I, J. USNM 858271. K. Protoconch, USNM 858264, bar = 100 μ m. Shell "A" is 2.7 mm tall; other shells printed to same scale.

Figure 8

Scanning electron micrographs of opercula and radula of *P. eremica* Hershler, sp. nov., USNM 858264. A–C. Opercula, bars = 250 μ m, 231 μ m, respectively ("B" same scale as "A"). D, E. Central radular teeth, bars = 10 μ m, 13.6 μ m, respectively. F. Lateral, inner marginal teeth, bar = 23.1 μ m. G. Section of radular ribbon, bar = 38 μ m. H. Lateral teeth, bar = 17.6 μ m. I. Outer marginal teeth, bar = 20 μ m.





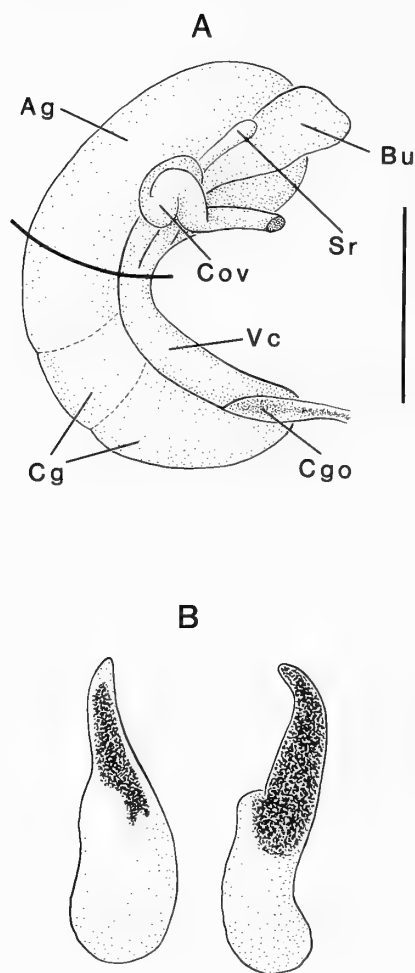


Figure 9

Genital morphology of *P. eremica* Hershler, sp. nov., USNM 858264. A. Distal female genitalia (left side). B. Penes (dorsal aspect). Bar = 0.5 mm. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Sr = seminal receptacle, Vc = ventral channel.

unnamed springs northeast of Horse Lake, Horse Lake basin, T. 33 N, R. 13 E, NE ¼ sec. 14, USNM 873138; Tule Patch Spring, Secret Valley, T. 32 N, R. 15 E, SE ¼ sec. 10, USNM 854569, USNM 858267, USNM 874053; unnamed spring, northern Secret Valley, T. 31 N, R. 15 E, NE ¼ sec. 3, USNM 858272; Sellicks Springs, Secret Valley, T. 31 N, R. 15 E, NW ¼ sec. 7, USNM

873210, USNM 874917; unnamed spring, Karlo Road, Secret Valley, T. 31 N, R. 15 E, NE ¼ sec. 3, USNM 874912; Sage Hen Spring, Smoke Creek Desert, T. 33 N, R. 16 E, NE ¼ sec. 35, USNM 858270; unnamed spring east of Sage Hen Spring, T. 33 N, R. 16 E, SW ¼ sec. 25, USNM 873411; unnamed spring southwest of Sage Hen Spring, T. 33 N, R. 16 E, NE ¼ sec. 35, USNM 858269; Big Spring, Smoke Creek Desert, T. 33 N, R. 16 E, NW ¼ sec. 1, USNM 858271, USNM 873392; unnamed springs, Shinn Ranch, Smoke Creek Desert, T. 33 N, R. 16 E, SW ¼ sec. 36, USNM 858268, USNM 873403; unnamed spring, east of Rush Creek Ranch, Smoke Creek Desert, T. 31 N, R. 17 E, SE ¼ sec. 11, USNM 858266.

Pyrgulopsis gibba Hershler, sp. nov.

(Figures 5C, 10–12)

Etymology: From Latin *gibber*, meaning swollen, and referring to enlarged penial lobe in this species.

Diagnosis: Shell ovate- to narrow-conic, medium-sized, umbilicate. Penial filament short; lobe enlarged. Penial ornament a terminal gland (often interrupted), Dg3 (sometimes absent), and ventral gland.

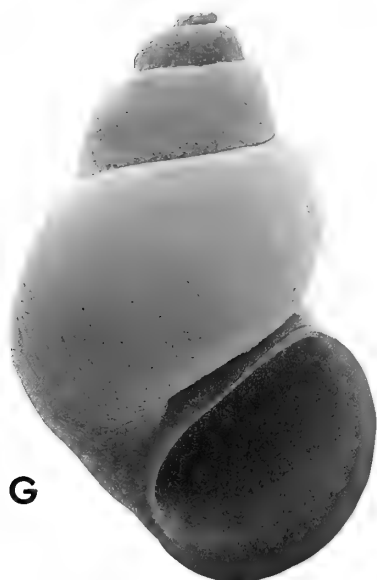
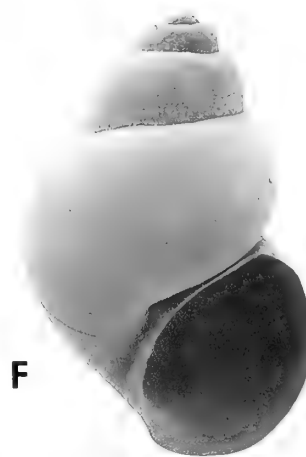
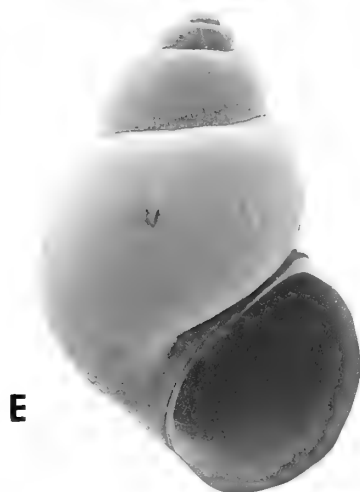
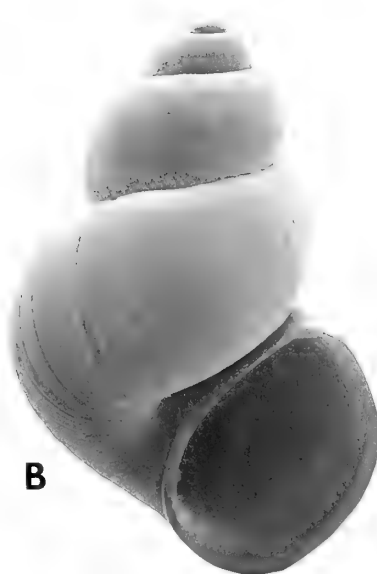
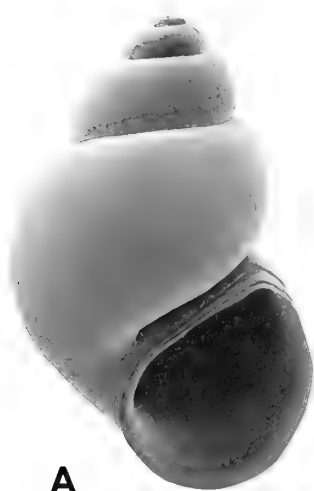
Description: Shell (Figures 5C, 10) ovate- to narrow-conic; height 2.7–3.5 mm; whorls 4.0–4.75. Protoconch (Figure 10H) about 1.5 whorls, early portion weakly wrinkled and incised with weak spiral grooves. Teleoconch whorls convex, slightly shouldered; sculpture of medium growth lines. Aperture ovate, narrowly adnate to or slightly separated from body whorl. Inner lip complete, thin, without columellar shelf. Outer lip thin, orthocline to slightly prosocline. Umbilicus narrowly rimate (near absent) to perforate. Periostracum tan-brown.

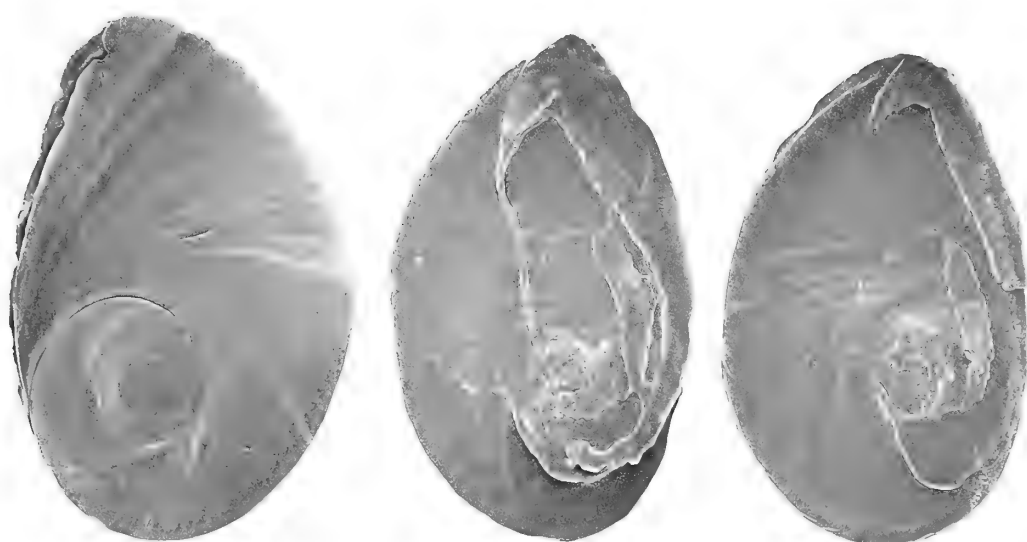
Operculum (Figure 11A–C) ovate, amber except for orange streaks in nuclear region; nucleus slightly eccentric; dorsal surface weakly frilled. Attachment scar margin often broadly thickened all around. Callus well developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radula ribbon elongate, about 0.86×0.15 mm, with about 65 rows of teeth. Central radular tooth (Figure 11D) trapezoidal, with highly indented dorsal edge; lateral cusps 5; central cusp spoon-like, slightly broader and considerably longer than laterals; basal cusps 1, short, with weak dorsal support. Basal process medium width; basal sockets deep. Lateral margins thickened, with medium to pronounced neck. Lateral tooth

Figure 10

Scanning electron micrographs of shells of *P. gibba* Hershler, sp. nov. A–E. USNM 858275. F. USNM 858274. G. USNM 858273. H. Protoconch, USNM 858275, bar = 136 μ m. Shell "A" is 2.7 mm; other shells printed to same scale.





A

B

C



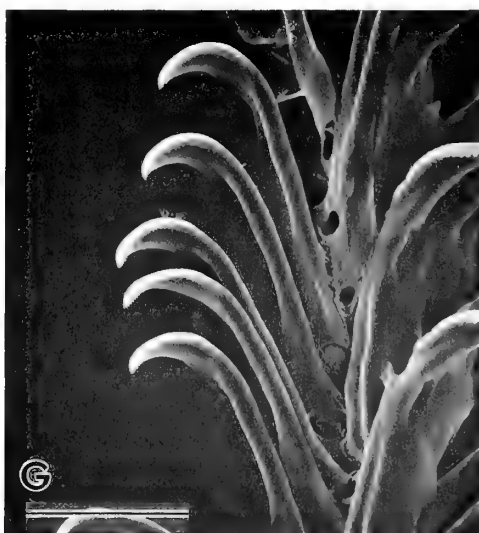
D



E



F



G

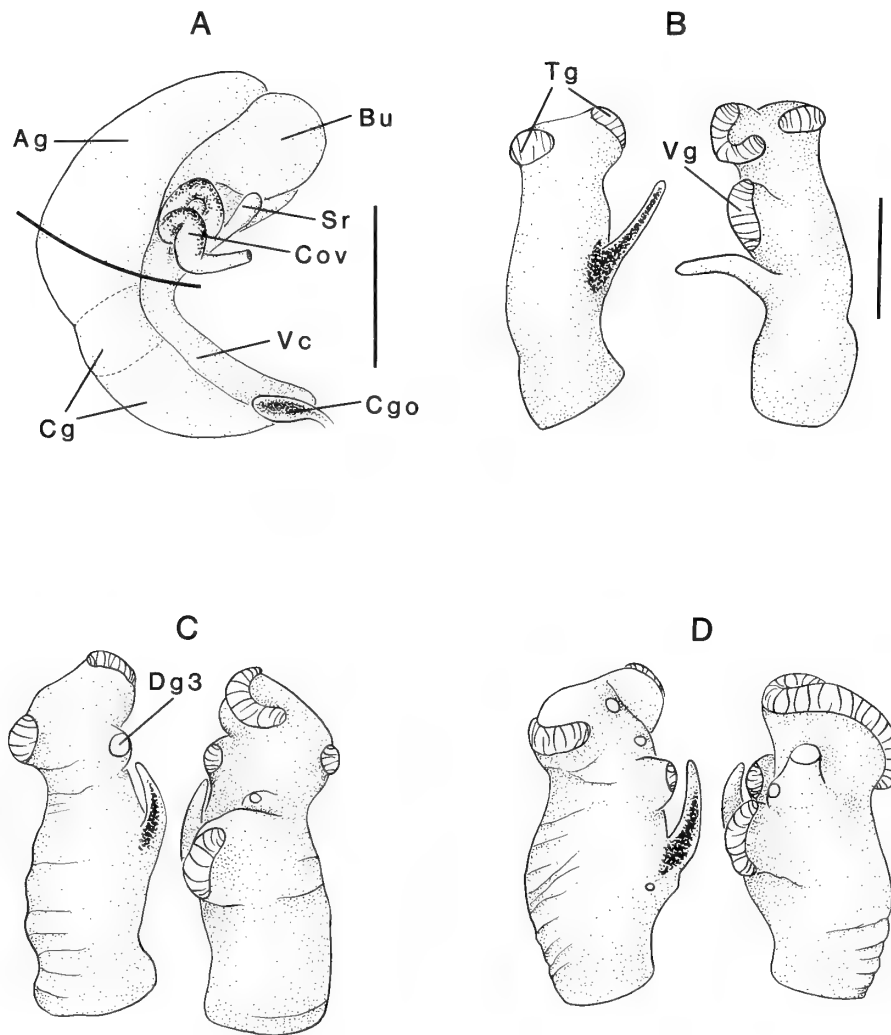


Figure 12

Genital morphology of *P. gibba* Hershler, sp. nov. A. Distal female genitalia (left side), USNM 858275, bar = 0.5 mm. B. Penis (dorsal aspect, left; ventral aspect, right), USNM 858275, bar = 0.5 mm. C. Ibid., USNM 858273. D. Ibid., USNM 858274. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Dg3 = dorsal gland, Sr = seminal receptacle, Tg = terminal gland, Vc = ventral channel, Vg = ventral gland.

(Figure 11E, F) formula 3-1-1; neck weakly developed; basal tongue well developed; outer wing about 170% of cutting edge length. Marginal teeth (Figure 11E-G) with about 23-36 (inner) and 28 (outer) cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles near pale to dark brown to black.

Snout medium to dark; distal lips sometimes pale. Foot pale to light along sides; anterior/posterior edges sometimes medium to dark. Opercular lobe dark along perimeter. Neck near pale to dark. Pallial roof, visceral coil black.

Ctenidial filaments 18-20, broad and tall; ctenidium

Figure 11

Scanning electron micrographs of opercula and radula of *P. gibba* Hershler, sp. nov., USNM 858275. A-C. Opercula, bars = 0.33 mm, 0.38 mm, respectively ("C" same scale as "B"). D. Central radular teeth, bar = 17.6 μ m. E. Lateral, inner marginal teeth, bar = 25 μ m. F. Lateral, marginal teeth, bar = 38 μ m. G. Outer marginal teeth, bar = 27 μ m.

slightly overlapping pericardium posteriorly. Osphradium small, centered slightly posterior to middle of ctenidial axis. Kidney with medium pallial bulge; renal gland longitudinal; kidney opening white. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland thin; overlapping rectum, pallial gonoducts, narrow portion of posterior pallial roof.

Distal female genitalia shown in Figure 12A. Ovary 0.5–0.75 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture a broad slit on slightly raised papilla, with short vestibule. Coiled oviduct lightly pigmented, of two short, oblique-circular, slightly overlapping coils. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix broadly ovate or saclike, slightly less than one-half of length of albumen gland, and slightly more than half of width of gland, with about 10–30% of length posterior to gland. Bursa duct narrow, about one-half of length of bursa copulatrix, well embedded in albumen gland. Seminal receptacle sometimes a slender pouch, sometimes lightly pigmented, about 20% of length of bursa copulatrix, overlapping or lateral to anterior portion of bursa copulatrix. Seminal receptacle duct medium length.

Testis 1.5 whorls, overlapping posterior stomach chamber. Prostate gland bean-shaped; near-circular in cross section; pallial section short. Pallial vas deferens with proximal twist. Penis (Figure 12B–D) large; base folded along inner edge; filament considerably shorter than base, narrow, tapering, parallel or slightly angled relative to long axis of base; lobe broadly rectangular, about as long as base, often bifurcate or swollen distally. Terminal gland elongate-transverse, usually curving onto both dorsal and ventral surfaces (most of length on latter), often interrupted, with units restricted to inner and outer portions of lobe, sometimes with a third, intermediate (ventral) unit or sometimes fused as single, elongate unit. Dg3 often present, either as small papule (sometimes double) or large, raised unit. Dorsal surface rarely with a very small proximal gland possibly representing reduced Dg1. Ventral gland large, elongate, borne on pronounced swelling, often accompanied by one to two smaller distal glands. Proximal two-thirds of filament darkly pigmented internally.

Type locality: Unnamed springs west of Fee Reservoir, Surprise Valley, Modoc County, California, T. 46 N, R. 17 E, NE $\frac{1}{4}$ sec. 20 (Figure 4C). Holotype, USNM 860643 (Figure 5C); paratypes, USNM 858275, collected by R. Hershler and D. Sada, 9 August 1990. Snails were commonly found in mud and scattered watercress in a series of degraded springs draining to a small meadow.

Remarks: This species is unique among members of the genus in having penial ornament of terminal gland, Dg3, and ventral gland. Affinities of the snail may lie with the group of western American species conforming in part to *Natricola* Gregg & Taylor, 1965, but it differs in lacking

Dg1 (although a very weak papule, perhaps conforming to this gland, rarely is present).

This snail occurs in the Great Basin of northeastern California (northern Surprise Valley, Duck Lake Valley; Figure 13).

Material examined: CALIFORNIA. LASSEN COUNTY: Unnamed spring, Old Marr Ranch, Tulead Canyon, Duck Flat, T. 37 N, R. 17 E, NE $\frac{1}{4}$ sec. 31, USNM 858273. MODOC COUNTY: Unnamed spring, northwest side of Lake Annie, northwest of Lake Annie Road, Surprise Valley, T. 47 N, R. 16 E, SW $\frac{1}{4}$ sec. 26, USNM 858274.

Pyrgulopsis greggi Hershler, sp. nov.

(Figures 5D, 14–16)

Amnicola.—Cooper, 1869:217 (In and about Ft. Tejon).

Etymology: This species is named in honor of the late Wendell O. Gregg, in recognition of his extensive research on the genus *Pyrgulopsis* in California and for his recognizing the distinctiveness of this snail when he collected it in 1964.

Diagnosis: Shell conical, small, umbilicate. Penis simple, blade-like; filament medium length, lobe absent. Penial ornament absent.

Description: Shell (Figures 5D, 14) conical; height, 1.6–2.6 mm; whorls 3.75–5.0. Protoconch (Figure 14F) about 1.5 whorls, early portion punctate and with several widely separated spiral lines. Teleoconch whorls convex, shouldered; sculpture of medium growth lines. Aperture ovate, narrowly adnate to (more commonly) slightly separated from body whorl. Inner lip complete, thin, without columellar shelf. Outer lip thin, orthocline. Umbilicus small, chinklike to broadly rimate.

Operculum (Figure 15A–C) broadly ovate, amber except for orange nuclear region; nucleus slightly eccentric; dorsal surface frilled. Attachment scar margin often broadly thickened all around. Callus well developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radula ribbon elongate, about 0.5 × 0.08 mm, with about 52 rows of teeth. Central radular tooth (Figure 15D) trapezoidal, with highly indented dorsal edge; lateral cusps 5–7; central cusp pointed, considerably broader and slightly longer than laterals; basal cusps 1, medium length, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened, with pronounced neck. Lateral tooth (Figure 15E, F) formula 4-1-4(5); neck weakly developed; basal tongue well developed; outer wing about 180% of cutting edge length. Marginal teeth (Figure 15E–G) each with about 22–26 cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles pale to medium grey to black (on proximal half). Snout medium to black. Foot pale, medium



Figure 13

Map showing distributions of *P. gibba* Hershler, sp. nov., *P. greggi* Hershler, sp. nov., and *P. ventricosa* Hershler, sp. nov. Symbols may refer to more than one locality.

grey or black along sides, with pigment especially heavy on anterior and posterior edges. Opercular lobe dark along margins. Neck pale to medium. Pallial roof, visceral coil mottled to uniformly black dorsally; pigment lighter on genital ducts.

Ctenidial filaments 18, medium height and width; ctenidium slightly overlapping pericardium posteriorly. Osphradium medium-sized, centered slightly posterior to middle of ctenidial axis. Kidney with medium pallial bulge; renal gland longitudinal; kidney opening white. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland thin; overlapping rectum, pallial gonoducts.

Distal female genitalia shown in Figure 16A. Ovary 1.0 whorl, partly overlapping posterior stomach chamber. Pallial albumen gland very short. Capsule gland slightly shorter than albumen gland. Genital aperture a broad slit with short anterior vestibule. Coiled oviduct of two small, overlapping, circular-oblique loops. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovate to clublike, medium length (33%) and width, with 20–25% of length posterior to albumen gland. Bursal duct medium width, about 150% of length of bursa copulatrix, partly embedded in albumen gland. Seminal receptacle pouchlike, sometimes folded, about 40% of length of bursa copulatrix,

anterior to or slightly overlapping bursa copulatrix. Seminal receptacle duct medium length.

Testis 2.0 whorls, overlapping entire stomach and extending to near edge of prostate gland. Prostate gland bean-shaped, narrow in cross section; pallial section medium. Pallial vas deferens with weak proximal bend. Penis (Figure 16B, C) small; base broadly to narrowly rectangular; filament about two-thirds of length of base, distally tapering, oriented parallel to long axis of base; lobe absent. Filament considerably narrower to sub-equal to base. Inner curvature of base lined with shallow folds. Proximal two-thirds of filament darkly pigmented internally.

Type locality: Grapevine Creek, Fort Tejon State Historical Park, Castac Valley, Kern County, California, T. 9 N, R. 19 W, NE ¼ section 16 (Figure 4D). Holotype, USNM 860641 (Figure 5D); paratypes, USNM 874139, collected by R. Hershler, 10 April 1991. Snails were commonly found in mud and watercress in this medium-sized, moderately impacted stream (ca. 1–2 m wide, 0.25 m deep).

Remarks: This species is restricted to Grapevine Creek drainage in the Upper Kern River basin (Figure 13).

Material examined: Topotypes, USNM 873418, WBM 4629, WBM 4689; Unnamed spring about 0.8 km north of above, T. 9 N, R. 19 W, NE ¼ sec. 9, USNM 873402, USNM 874140.

Pyrgulopsis longae Hershler, sp. nov.

(Figures 5E, 17–19)

Etymology: The species name refers to distribution of the snail within Long Valley.

Diagnosis: Shell ovate- to narrow-conic, medium-sized, umbilicate. Penial filament short, lobe medium-sized. Penial ornament a short penial gland and small terminal gland.

Description: Shell (Figures 5E, 17) ovate- to narrow-conic; height 2.2–3.0 mm; whorls 4.0–4.75. Protoconch (Figure 17F) 1.5 whorls, near smooth. Teleoconch whorls convex, slightly shouldered; sculpture of weak growth lines. Aperture ovate, usually slightly separated from body whorl. Inner lip complete, thin, without columellar shelf. Outer lip thin, orthocline. Umbilicus small, chinklike to broadly rimate. Periostracum dark tan.

Operculum (Figure 18A–C) narrowly ovate, amber except for reddish nuclear region; nucleus highly eccentric; dorsal surface weakly frilled. Attachment scar margin often well thickened all around. Callus well developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radular ribbon elongate, about 0.65 × 0.10 mm, with about 70 rows of teeth. Central radular tooth (Figure 18D, E) trapezoidal, with highly indented dorsal edge; lateral cusps 5; central cusp rounded, considerably broader and slightly longer than laterals; basal cusps 1, elongate, with moderate dorsal sup-

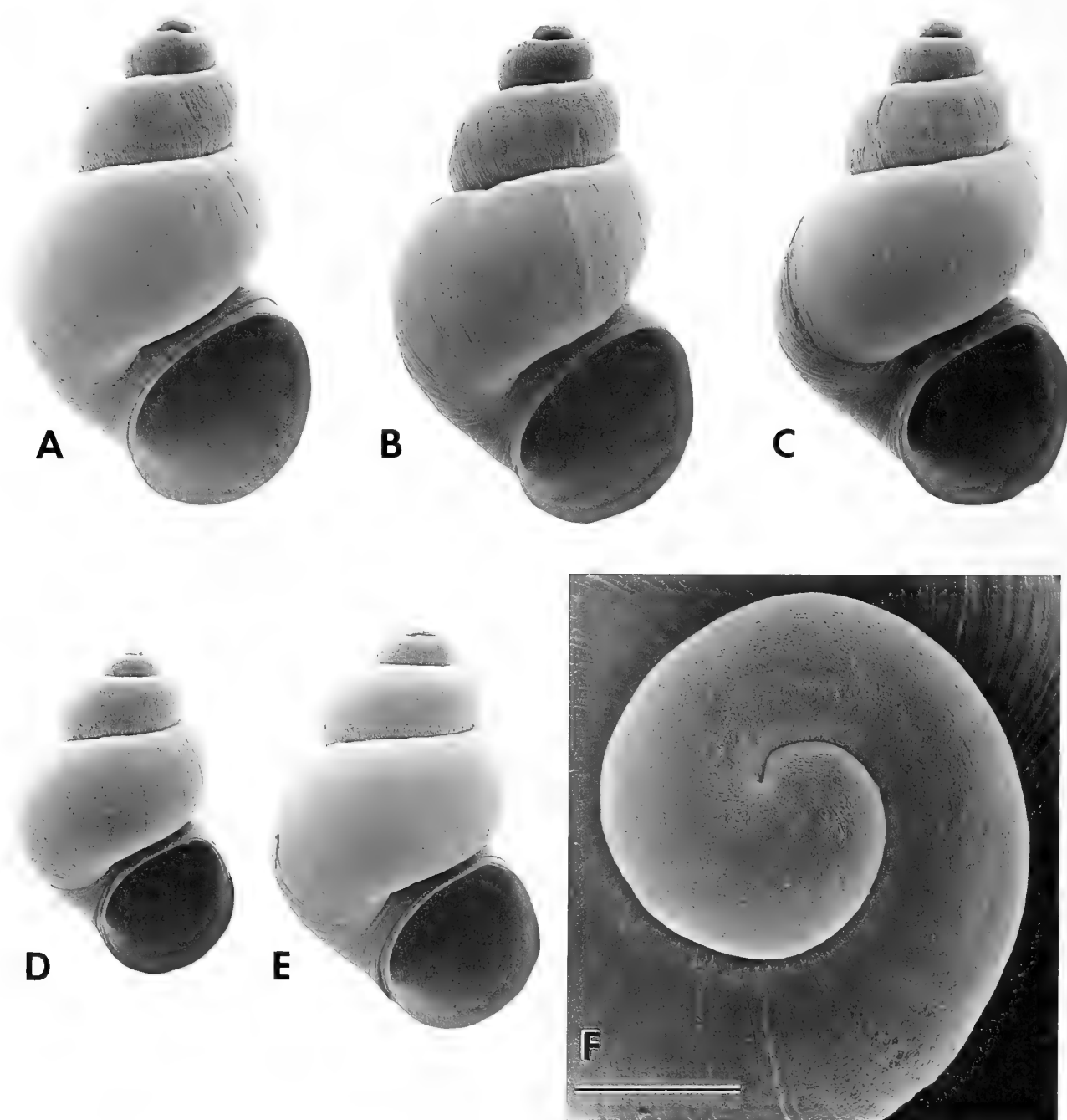
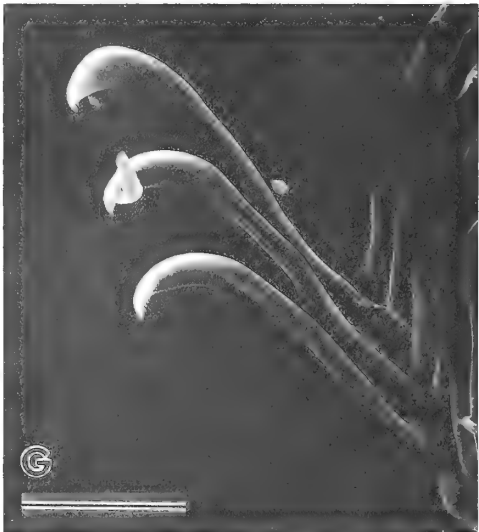
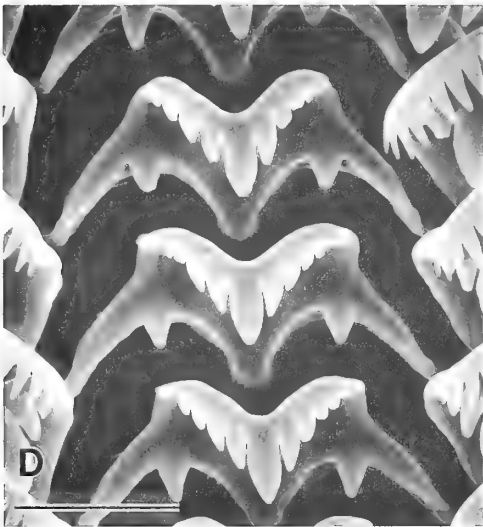
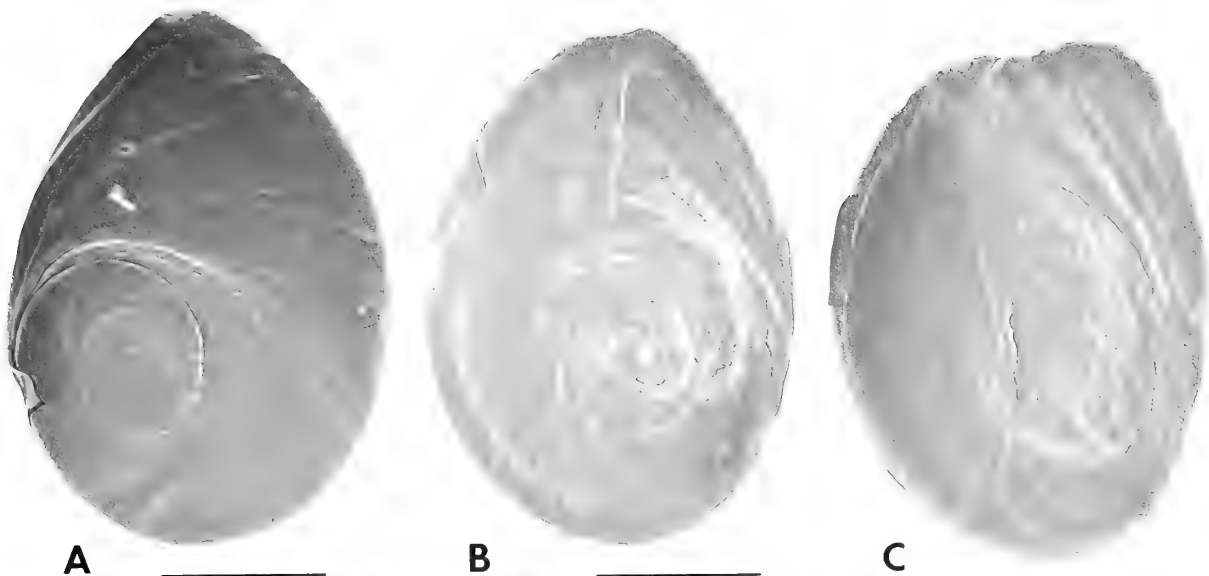


Figure 14

Scanning electron micrographs of shells of *P. greggi* Hershler, sp. nov. A–C. USNM 874139. D, E. USNM 874140. F. Protoconch, USNM 874139, bar = 120 μ m. Shell “A” is 2.3 mm tall; other shells printed to same scale.

Figure 15

Scanning electron micrographs of opercula and radula of *P. greggi* Hershler, sp. nov., USNM 873418. A–C. Opercula, bars = 250 μ m, 270 μ m, respectively (“C” same scale as “B”). D. Central radular teeth, bar = 10 μ m. E, F. Lateral, inner marginal teeth, bars = 17.6 μ m. G. Outer marginal teeth, bar = 17.6 μ m.



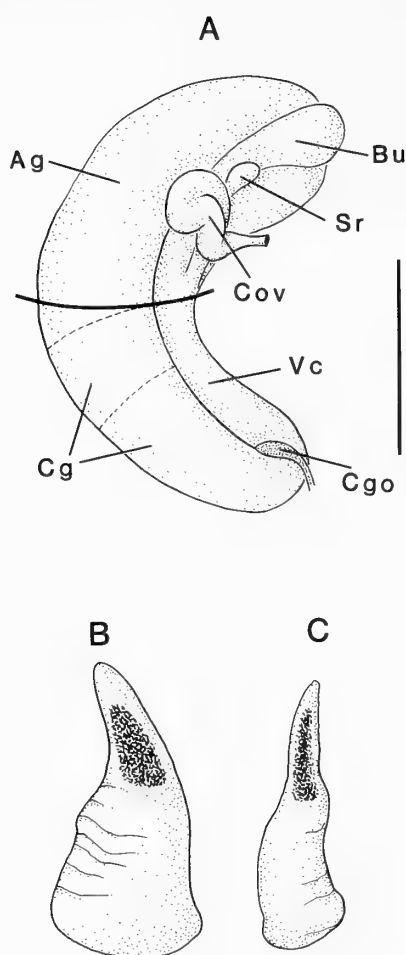


Figure 16

Genital morphology of *P. greggi* Hershler, sp. nov. A. Distal female genitalia (left side), USNM 874139. B, C. Penes (dorsal aspect), USNM 874139 (left), USNM 874140 (right). Bar = 0.5 mm. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Sr = seminal receptacle, Vc = ventral channel.

port. Basal process narrow; basal sockets deep. Lateral margins thickened, with pronounced neck. Lateral tooth (Figure 18E) formula 4-1-4; neck well developed; basal tongue well developed; outer wing about 150% of cutting edge length. Marginal teeth (Figure 18E-G) with about 24 (inner) and 28 (outer) cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles with medium grey to black pigment proximally. Snout light to medium grey. Foot light along sides; anterior edge light to medium. Opercular lobe usually black along margins. Neck pale to light grey. Pallial roof, visceral coil uniformly black.

Ctenidial filaments 22, medium height and width; ctenidium slightly overlapping pericardium. Osphradium

medium-sized, centered slightly posterior to middle of ctenidial axis. Kidney with medium pallial bulge; renal gland longitudinal; kidney opening white. Rectum straight, broadly overlapping genital duct. Hypobranchial gland medium thickness; overlapping rectum, pallial gonoducts, roof of pallial cavity alongside rectum.

Distal female genitalia shown in Figure 19A. Ovary 0.75–1.0 whorl, overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland shorter than albumen gland. Genital aperture a broad slit without vestibule. Coiled oviduct a small proximal kink or twist followed by elongate horizontal coil. Oviduct and bursal duct join just behind pallial wall. Bursa copulatrix ovoid-pyriform, medium length and width, with about one-half of length posterior to albumen gland. Bursal duct narrow (broadening distally), about two-thirds of length of bursa copulatrix, partly embedded in albumen gland. Seminal receptacle globular-pyriform, sometimes folded, about one-half of length of bursa copulatrix, overlapping anterior half of bursa copulatrix. Seminal receptacle duct short.

Testis 1.25 whorls, overlapping posterior stomach chamber. Prostate gland bean-shaped, narrow in cross section; pallial section very short to absent. Pallial vas deferens without proximal twist. Penis (Figure 19B) large; base broadly rectangular; filament short, tapering distally; lobe medium-sized, tapering distally. Penial gland a short strip on base of filament. Terminal gland small, transverse-circular, usually borne on ventral surface. Proximal half of penial filament with dark internal pigment; distal half of penis base with scattered black granules.

Type locality: Unnamed spring about 4.8 km west-southwest of Hallelujah Junction, Long Valley, Lassen County, California, T. 22 N, R. 17 E, SW $\frac{1}{4}$ sec. 9 (Figure 4E). Holotype, USNM 860642 (Figure 5E); paratypes, USNM 858262, collected by R. Hershler and D. Sada, 3 August 1990. Snails were commonly found on stones and in watercress of this large spring, which was situated adjacent to a residence and had been recently excavated.

Remarks: This species is known only from the type locality in the southern end of the Honey Lake basin (Figure 6).

Pyrgulopsis taylori Hershler, sp. nov.

(Figures 5F, 20–22)

Etymology: This species is named in honor of Dwight W. Taylor, in recognition of his many years of fieldwork and associated research on hydrobiids both in California and throughout the western United States.

Diagnosis: Shell ovate- to narrow-conic or pupiform, small, umbilicate. Penial filament elongate; lobe short. Penial ornament a terminal gland and occasionally a small penial gland.

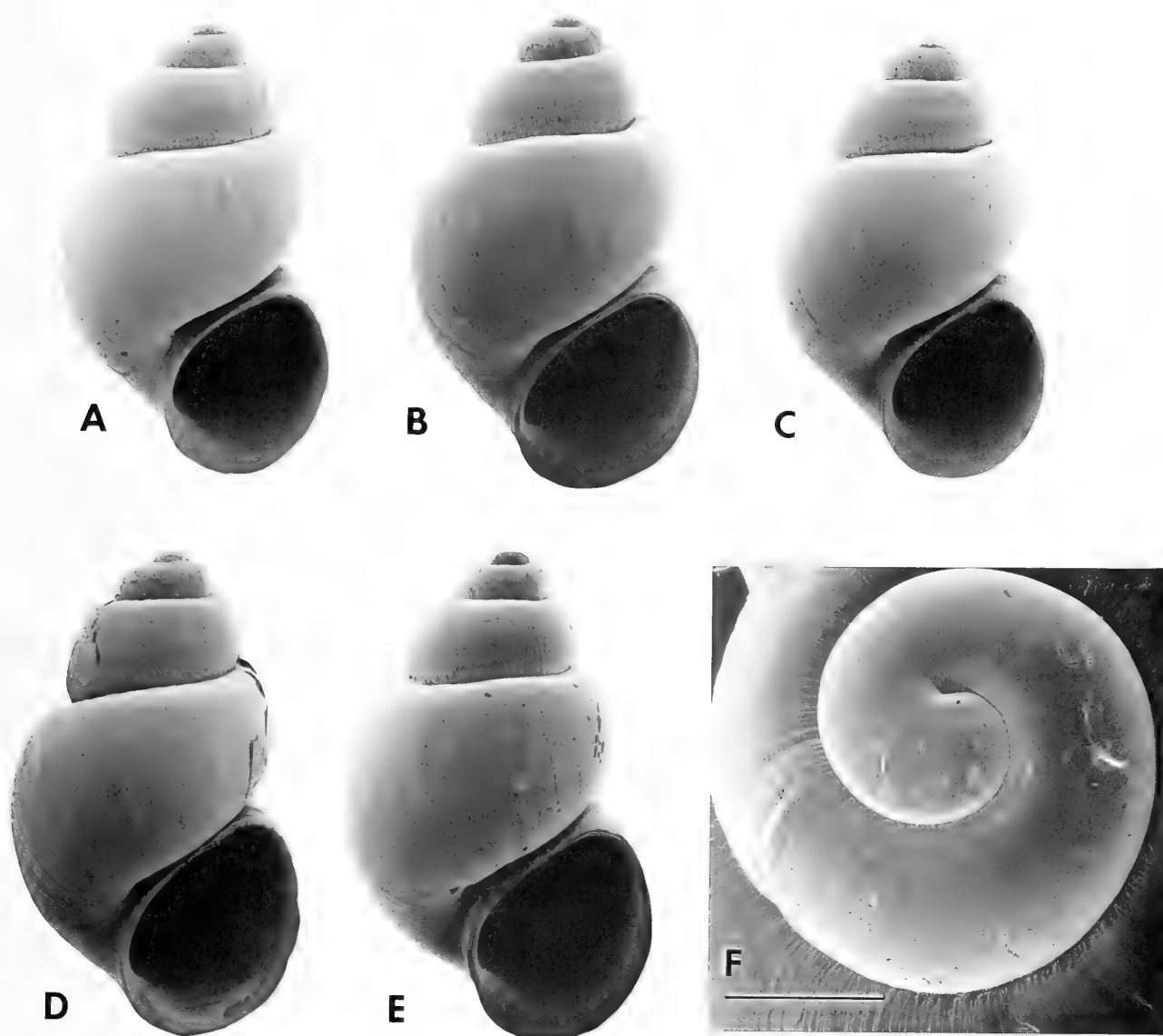


Figure 17

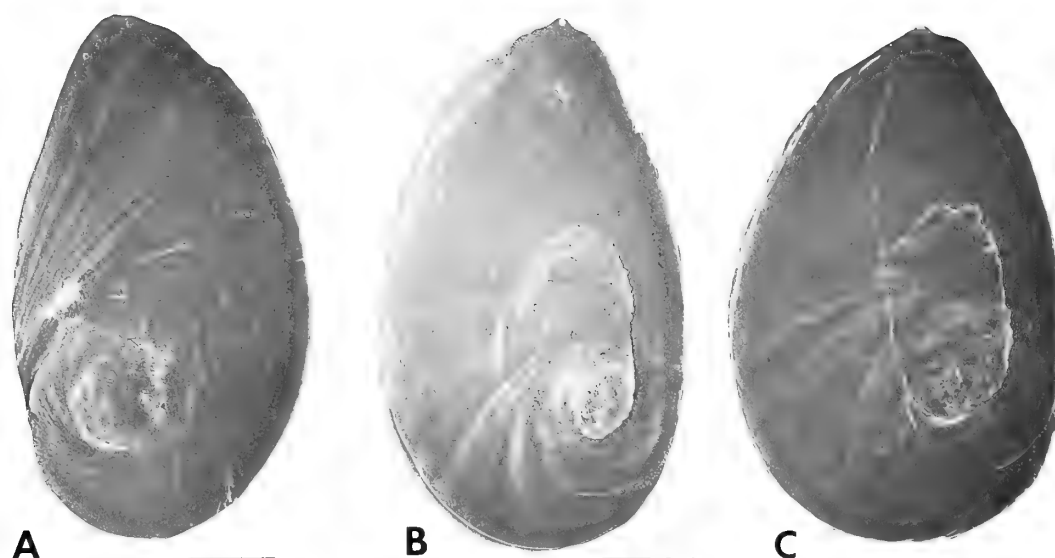
Scanning electron micrographs of shells of *P. longae* Hershler, sp. nov., USNM 858262. F. Protoconch, bar = 136 μ m. Shell "A" is 2.5 mm tall; other shells printed to same scale.

Description: Shell (Figures 5F, 20) ovate- to narrow-conic or pupiform; height 2.0–3.3 mm; whorls 4.0–5.25. Protoconch (Figure 20I) about 1.5 whorls, early portion wrinkled, with a few weak spiral striae. Teleoconch whorls near flat to medium convexity, narrowly shouldered; sculpture of strong growth lines crossed by very weak spiral striae. Aperture ovate-pyriform, often enlarged, broadly adnate to slightly separated from body whorl. Inner lip complete, thin or slightly thickened, columellar shelf often pronounced. Outer lip thin or slightly thickened, ortho-

cline. Umbilicus small, chinklike or perforate. Periostracum tan.

Operculum (Figure 21A–C) narrowly ovate, very thin, light amber; nucleus highly eccentric; dorsal surface weakly frilled. Attachment scar usually only weakly thickened along inner edge. Callus weakly developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radula ribbon moderately elongate, about 0.9×0.09 mm, with about 60 rows of teeth. Central radular tooth (Figure 21D) trapezoidal,



with well-indented dorsal edge; lateral cusps 5; central cusp pointed, considerably broader and longer than laterals; basal cusps 1, short, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins thickened, with medium neck. Lateral tooth (Figure 21E) formula 3-1-3(4); neck very weakly developed; outer wing 150–180% of cutting edge length. Marginal teeth (Figure 21F, G) with about 17–22 (inner) and 19–20 (outer) cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

Cephalic tentacles pale or with light grey patch proximally. Snout pale to medium grey. Foot pale or with light grey patch along anterior edge. Opercular lobe black along inner edge. Neck pale or very light grey. Pallial roof, visceral coil variably pigmented brown to black, rarely uniformly so.

Ctenidial filaments about 17, short, narrow, weakly pleated; ctenidium not overlapping pericardium posteriorly. Osphradium medium-sized, positioned centrally or slightly posterior to middle of ctenidial axis. Kidney with medium-sized pallial bulge; renal gland longitudinal; kidney opening white. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland thin; overlapping rectum, pallial gonoducts.

Distal female genitalia shown in Figure 22A. Ovary 0.5–0.75 whorl, slightly overlapping posterior stomach chamber. Pallial albumen gland short. Capsule gland slightly shorter than albumen gland. Genital aperture a large subterminal pore, with very short vestibule. Coiled oviduct a small, near circular coil preceded by proximal twist. Oviduct and bursal duct join well behind pallial wall. Bursa copulatrix simply ovate, up to one-third length of albumen gland, and one-half width of gland, with about 50–65% of length posterior to gland. Bursa duct medium width, well embedded in albumen gland. Seminal receptacle pouchlike, sometimes folded, 50–70% of length of bursa copulatrix, partly overlapping anterior portion of bursa copulatrix. Seminal receptacle duct medium length.

Testis 1.5–2.0 whorls, overlapping posterior and portion of anterior stomach chambers. Prostate gland narrowly bean-shaped; oval in cross section; pallial section medium length. Pallial vas deferens with weak proximal bend. Penis (Figure 22B, C) medium-sized; edges unfolded; filament sometimes as long as base, narrow, tapering, parallel to strongly oblique to long axis of base; lobe hemispherical, short (rarely near absent). Terminal gland circular or ovate, usually positioned on ventral surface. Penial gland small (often absent), near circular, positioned near base of filament. Filament darkly pigmented internally.

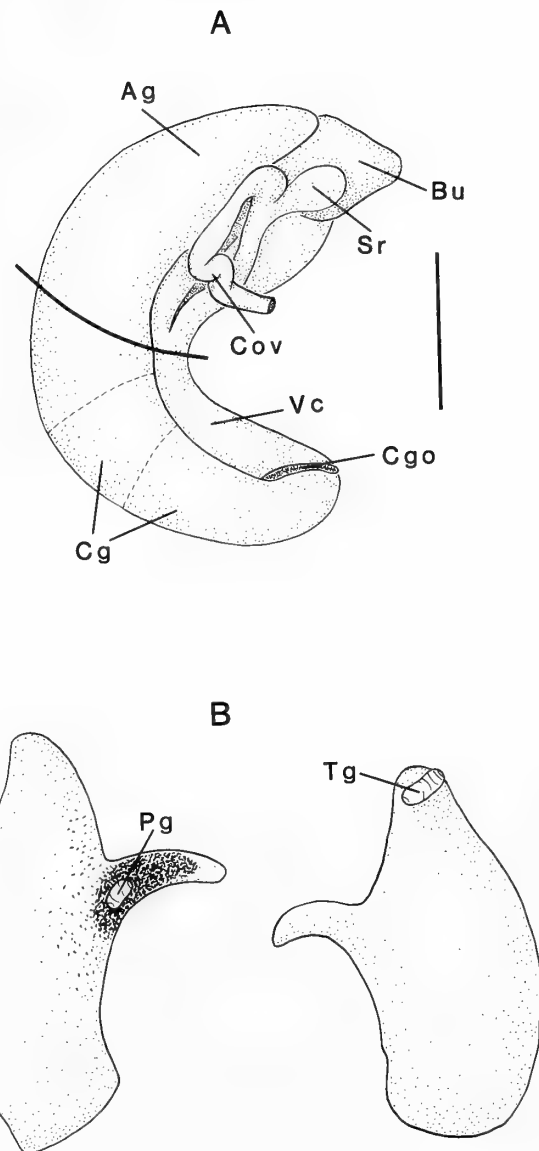
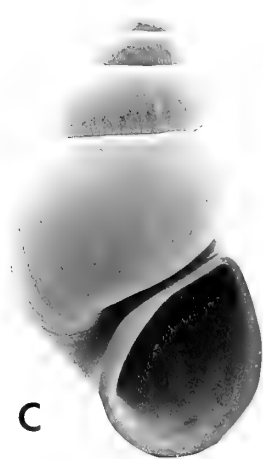


Figure 19

Genital morphology of *P. longae* Hershler, sp. nov., USNM 858262. A. Distal female genitalia (left side). B. Penis (dorsal aspect, left; ventral aspect, right). Bar = 0.5 mm. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Pg = penial gland, Sr = seminal receptacle, Tg = terminal gland, Vc = ventral channel.

Figure 18

Scanning electron micrographs of opercula and radula of *P. longae* Hershler, sp. nov., USNM 858262. A–C. Opercula; bars = 0.33 mm, 0.38 mm, 0.30 mm, respectively. D. Central radular teeth, bar = 15 μ m. E. Central, lateral, marginal teeth, bar = 25 μ m. F, G. Marginal teeth, bars = 23.1 μ m, 30 μ m, respectively.



Type locality: Unnamed spring tributary to San Luis Obispo Creek, 4.8 km north of San Luis Obispo, east of HW 101, San Luis Obispo County, California, T. 30 S, R. 13 E, SE $\frac{1}{4}$ sec. 7 (Figure 4G). Holotype, USNM 860646 (Figure 5F); paratypes, USNM 883792, collected by R. Hershler, 6 May 1994. Snails were found in moderate abundance on rocks and in leaf litter along this small spring brook, which was in fairly good condition despite some recreational impacts and historic diversion near the source.

Remarks: This snail is known only from San Luis Obispo Creek drainage along the south-central California coast (Figure 6).

Material examined. CALIFORNIA. SAN LUIS OBISPO COUNTY: topotypes, USNM 874459, WBM 3865; Unnamed spring tributary to Brizzolari Creek, 1.6 km north of California Polytechnic State University, San Luis Obispo, T. 30 S, R. 12 E, unsurveyed, USNM 883789; Chorro Creek, Camp San Luis Obispo, T. 30 S, R. 12 E, NW $\frac{1}{4}$ sec. 3, USNM 854590; Unnamed spring tributary to Morro Creek, west side of HW 41, T. 29 S, R. 11 E, SE $\frac{1}{4}$ sec. 2, USNM 883788.

Pyrgulopsis ventricosa Hershler, sp. nov.

(Figures 5G, 23–25)

Pomatiopsis intermedia.—Cooper, 1876:36 ("near Clear Lake").

Etymology: From Latin *ventricosus*, meaning bulging, and referring to the well-developed ventral penial glands in this species.

Diagnosis: Shell ovate- to narrow-conic, medium-sized, umbilicate. Penial filament, lobe medium-sized. Penial ornament a transverse terminal gland, elongate penial gland, elongate Dg1, short Dg2, variable Dg3, an additional elongate dorsal gland, and two prominent ventral glands.

Description: Shell (Figures 5G, 23) ovate- to narrow-conic; height 2.2–2.6 mm; whorls 4.0–4.5. Protoconch (Figure 23F) about 1.25 whorls, early portion strongly wrinkled with occasional spiral lines. Teleoconch whorls convex, strongly shouldered; sculpture of weak growth lines and faint spiral striae. Aperture ovate, adnate to well separated from body whorl. Inner lip complete, thin, without columellar shelf. Outer lip thin, orthocline. Umbilicus

narrow. Periostracum tan; shell usually covered with thick organic deposits.

Operculum (Figure 24A–C) ovate, amber with reddish center of attachment scar; nucleus eccentric; dorsal surface frilled. Attachment scar margin broadly thickened all around. Callus well developed.

Buccal mass medium-sized; radular sac protruding behind buccal mass as short coil. Radula ribbon moderately elongate, about 0.65×0.11 mm, with about 50 rows of teeth. Central radular tooth (Figure 24D) trapezoidal, with medium to highly indented dorsal edge; lateral cusps 4–5; central cusp pointed, considerably broader and longer than laterals; basal cusps 1, short, with weak dorsal support. Basal process narrow; basal sockets deep. Lateral margins weakly thickened, with weak neck. Lateral tooth (Figure 24E) formula 3-1-4; neck weakly developed; basal tongue well developed; outer wing 160–180% of cutting edge length. Marginal teeth (Figure 24E–G) with about 16–20 (inner) and 20–23 cusps; cusps extending onto outer edge of teeth. Stomach caecum small.

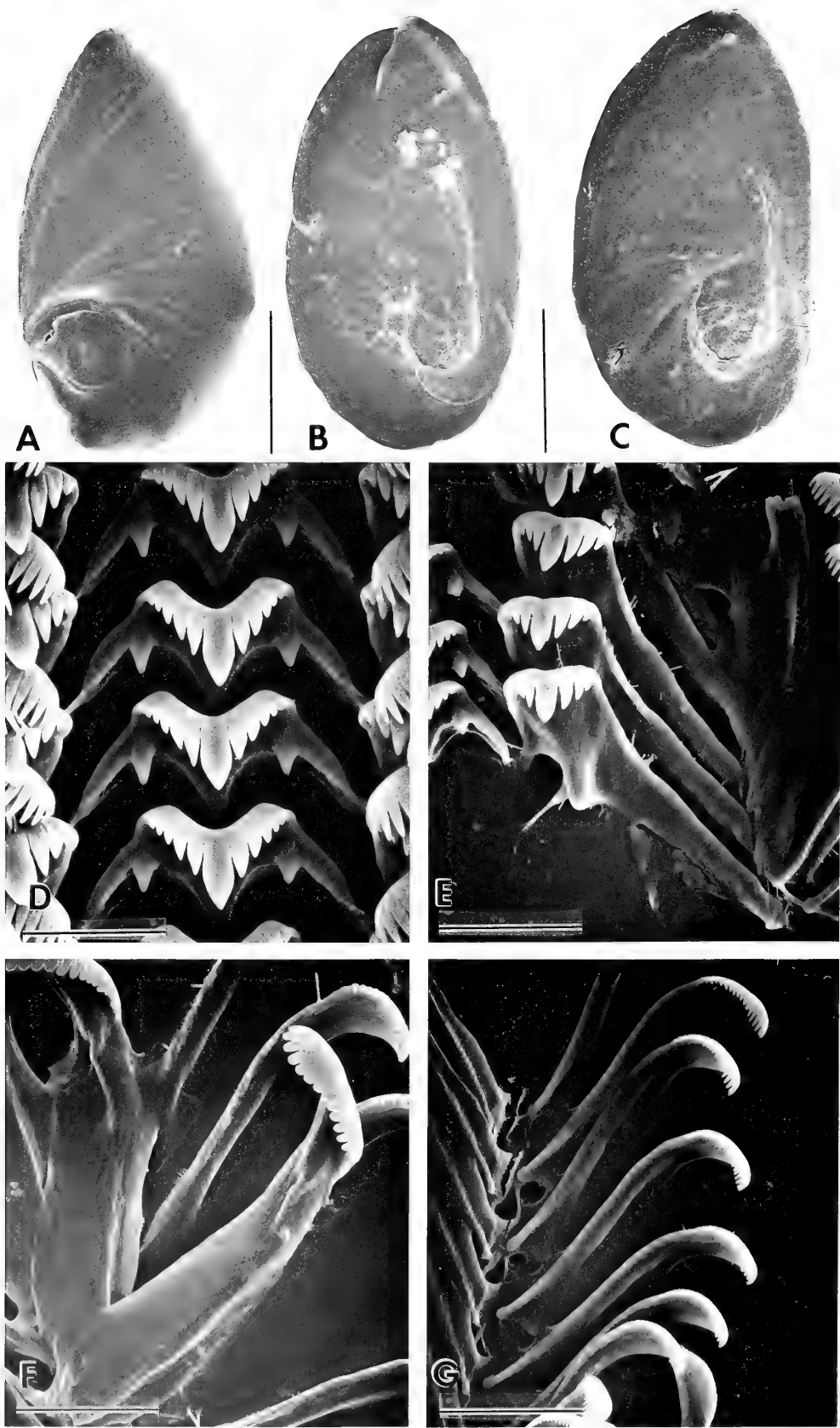
Cephalic tentacles light grey to black; pigment sometimes a longitudinal band on pale background. Snout grey to black, rarely red. Foot grey to black along anterior end, sometimes similarly pigmented along rest of margin, otherwise pale. Opercular lobe black along inner edge, lighter along rest of margin. Neck pale to near black. Pallial roof mottled to near uniform black; visceral coil slightly lighter.

Ctenidial filaments 22, medium width, tall; ctenidium slightly overlapping pericardium posteriorly. Osphradium small, centered well posterior to middle of ctenidial axis. Kidney with medium pallial bulge; renal gland longitudinal; kidney opening white. Rectum straight, broadly overlapping genital ducts. Hypobranchial gland thin; overlapping rectum, pallial gonoducts.

Distal female genitalia shown in Figure 25A. Ovary 1.0 whorl, abutting posterior edge of stomach. Pallial albumen gland short. Capsule gland about as long as or slightly longer than albumen gland. Genital aperture a broad slit; vestibule absent or very weakly developed. Coiled oviduct circular-horizontal, simple or kinked near mid-point. Oviduct and bursal duct join slightly behind pallial wall. Bursa copulatrix ovate, sometimes with blunt anterior edge, 80–110% length of albumen gland, as wide or slightly narrower than albumen gland, with almost entire length posterior to gland. Bursal duct narrow, short (about one-fourth to one-third length of bursa copulatrix), weakly embedded in albumen gland. Seminal receptacle a small pouch, less than one-fourth length of bursa copulatrix, overlapping anterior portion of bursa copulatrix. Seminal receptacle duct medium length.

Figure 20

Scanning electron micrographs of shells of *P. taylori* Hershler, sp. nov. A–E, USNM 883792. F–H, USNM 883789. I. Protoconch, USNM 883792, bar = 136 μ m. Shell "A" is 2.2 mm tall; other shells printed to same scale.



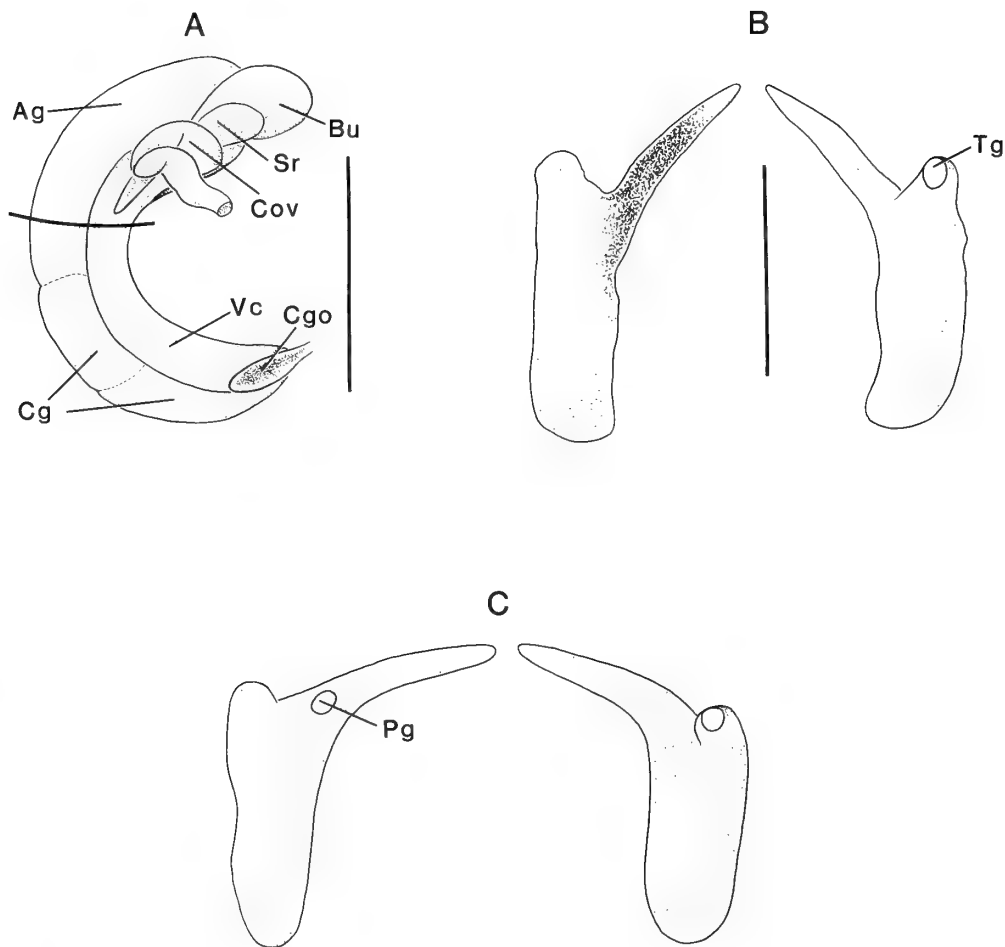


Figure 22

Genital morphology of *P. taylori* Hershler, sp. nov., USNM 883792. A. Distal female genitalia (left side). Bar = 0.5 mm. B. C. Penes (dorsal aspect, left; ventral aspect, right). Bar = 0.5 mm. Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Pg = penial gland, Sr = seminal receptacle, Tg = terminal gland, Vc = ventral channel.

Testis, 1.5 whorls, overlapping posterior and portion of anterior stomach chambers. Prostate gland bean shape; narrow oval in cross section; pallial section short. Pallial vas deferens with very large proximal loop. Penis (Figure 25B–D) large; base rectangular, weakly folded along inner edge; filament considerably shorter than base, medium width, tapering, slightly oblique to long axis of base; lobe slightly tapering distally, shorter than filament. Terminal

gland transverse, usually interrupted into two distinct units (rarely with third intermediate glandular dot), usually coursing over dorsal and ventral surfaces. Penial gland elongate, covering most of length of filament. Dg1 elongate, extending along length of base near outer edge, sometimes fused with either Dg3 or additional dorsal glands. Dg2 short. Dg3 dotlike to large, borne on pronounced swelling. Dorsal penis also with an additional elongate gland (as

Figure 21

Scanning electron micrographs of opercula and radula of *P. taylori* Hershler, sp. nov., USNM 883792. A–C. Opercula; bars = 231 μm , 250 μm . “C” printed to same scale as “A.” D. Central radular teeth, bar = 12 μm . E. Lateral teeth, bar = 15 μm . F. Inner marginal teeth, bar = 12 μm . G. Outer marginal teeth, bar = 17.6 μm .

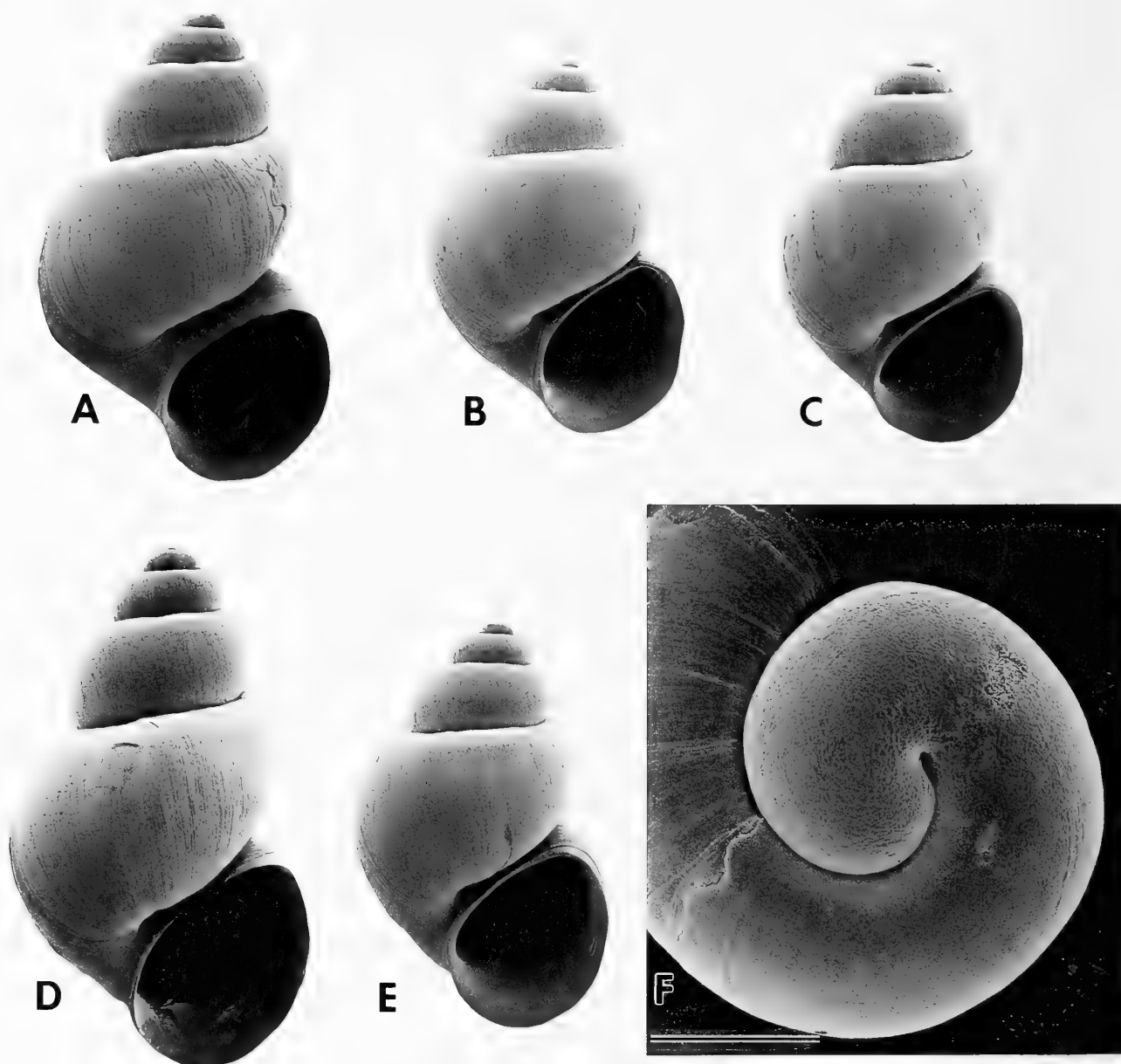
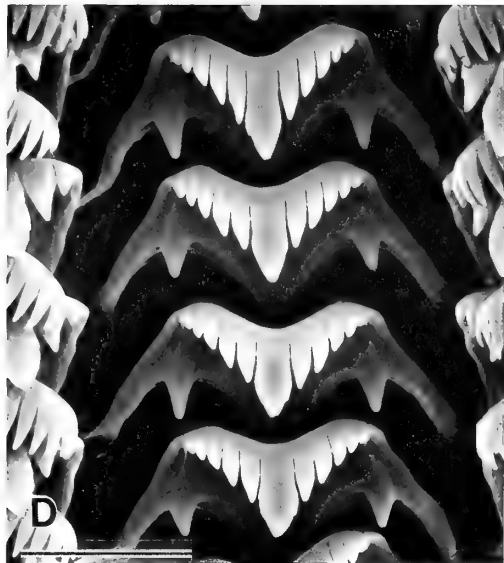
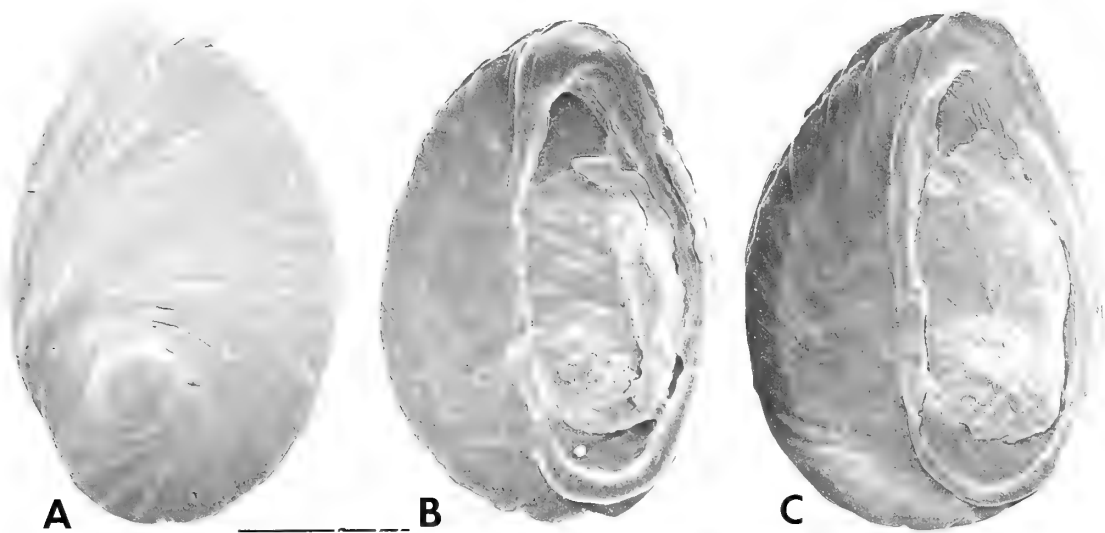


Figure 23

Scanning electron micrographs of shells of *P. ventricosa* Hershler, sp. nov., USNM 883790. F. Protoconch, bar = 120 μ m. Shell "A" is 2.9 mm tall; other shells printed to same scale.

Figure 24

Scanning electron micrographs of opercula and radula of *P. ventricosa* Hershler, sp. nov., USNM 883790. A-C. Opercula, bar = 0.30 mm. D. Central radular teeth, bar = 12 μ m. E. Central, lateral, inner marginal teeth, bar = 17.6 μ m. F. Inner marginal teeth, bar = 17.6 μ m. G. Inner and outer marginal teeth, bar = 23.1 μ m.



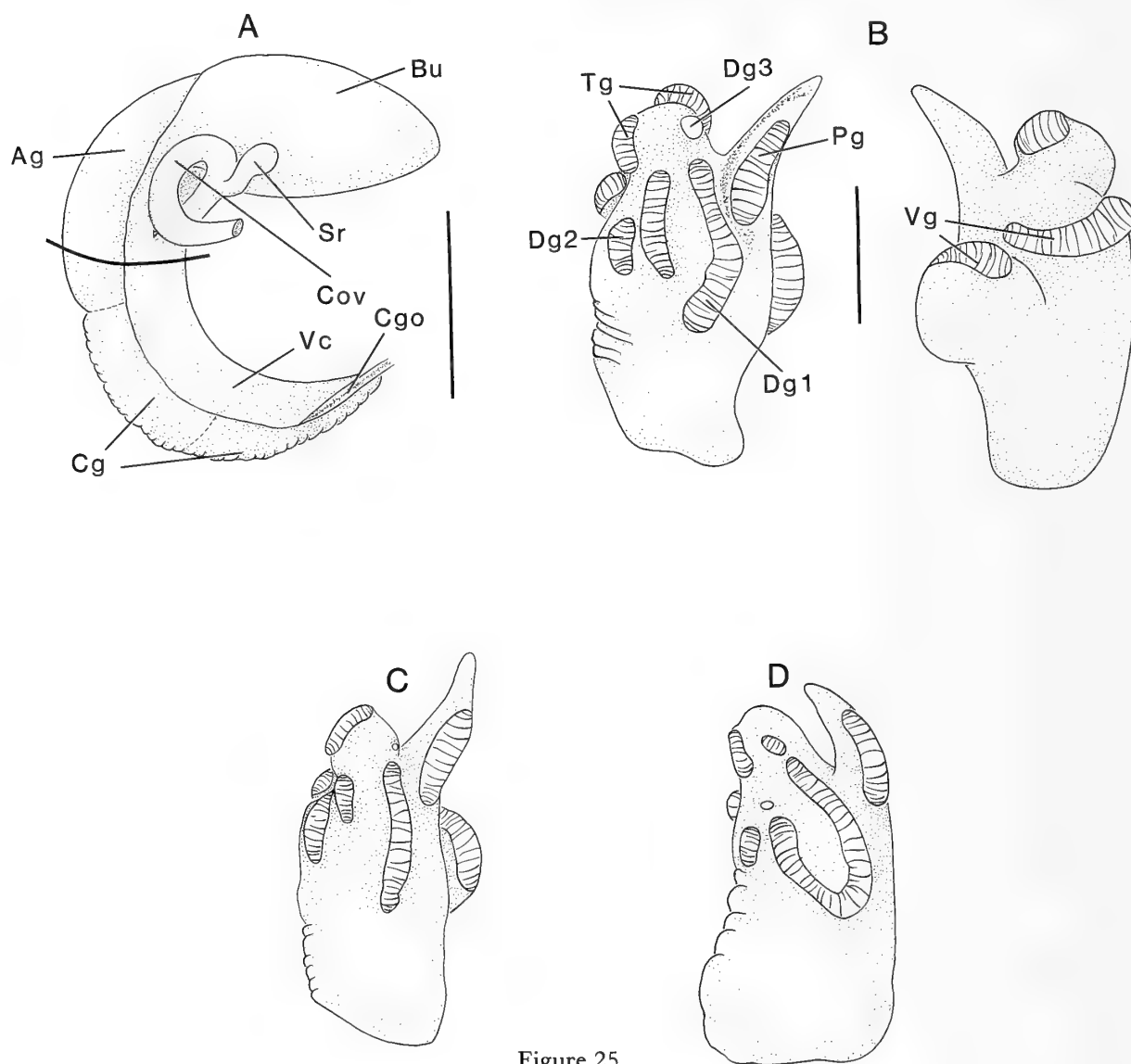


Figure 25

Genital morphology of *P. ventricosa* Hershler, sp. nov., USNM 883790. A. Distal female genitalia (left side). Bar = 0.5 mm. B. Penis (dorsal aspect, left; ventral aspect, right). Bar = 0.5 mm. C, D. Penes (dorsal aspects). Scale as in "B." Ag = albumen gland, Bu = bursa copulatrix, Cg = capsule gland, Cgo = capsule gland opening, Cov = coiled oviduct, Dg1 = gland along right edge, Dg2 = gland along left distal edge, Dg3 = gland along right edge of lobe, Pg = penial gland, Sr = seminal receptacle, Tg = terminal gland, Vc = ventral channel, Vg = ventral gland.

well as one to two small glandular dots) centrally positioned between Dg1 and Dg3, apparently sometimes fused with former. Ventral penis with distal transverse gland (rarely interrupted into two units) borne on low swelling and large, near central gland borne on tall swelling. Filament darkly pigmented internally along most of length.

Type locality: Unnamed creek, Seigler Canyon, 7.4 km south of HW 29 along Seigler Canyon Road, Clear Lake basin, Lake County, California, T. 12 N, R. 7 W, NE ¼ sec. 19 (Figure 4F). Holotype, USNM 860647 (Figure

5G); paratypes, USNM 883790, collected by R. Hershler and S. Ellis, 3 May 1994. Snails were commonly found on vegetation in this small (1 m wide, 3 cm deep), spring-fed stream, which had been diverted and additionally impacted by residential activities.

Remarks: This species is similar to the most derived members of the "*californiensis* series" (see above), which are characterized in part by possession of a full complement of glands on the penis (Pg, Tg, Dg1-3) and an enlarged bursa copulatrix. Of the members of this group, only *P.*

californiensis, from coastal regions along southern California, and *P. wongi*, from Owens River drainage and several other basins to the east of Sierra Nevada, share with our species two well-developed ventral glands (Vg) and a very small seminal receptacle. *Pyrgulopsis ventricosa* shares with *P. californiensis* an ovate-narrow conic shell and short bursal duct, but is distinguished by penial features, including the generally longitudinal (not transverse) orientation of Dg1, shorter Dg2, fewer and smaller additional dorsal glands, and more pronounced proximal ventral gland.

Late Cenozoic hydrobiids from the Cache Formation in the Clear Lake basin have been provisionally allocated to *Hydrobia andersoni* Arnold, 1909 (Taylor, 1966 and references cited therein; Rymer et al., 1988), which in turn was described from fossils of the Tulare Formation in Kettleman Hills, located near the southern end of San Joaquin Valley. Although I have not seen Cache Formation material and thus cannot ascertain possible conspecificity with our snail, this novelty is clearly distinguished from typical *H. andersoni* by its smaller, squatter shell and shallower sutures.

This species is restricted to Seigler Creek drainage in the south end of the Clear Lake basin (Figure 13). Although unpublished historic records suggested that the snail was formerly widespread in this region (at least until the 1970s), I was able to locate only one other living colony a short distance from the type locality in 1994.

Material examined: CALIFORNIA. LAKE COUNTY: Unnamed spring, Seigler Canyon, T. 12 N, R. 7 W, NE $\frac{1}{4}$ sec. 19, USNM 873134; Seigler Springs, T. 12 N, R. 8 W, NE $\frac{1}{4}$ sec. 24, USNM 874925.

ACKNOWLEDGMENTS

I thank F. G. Hochberg and P. Scott (Santa Barbara Museum of Natural History) for lending specimens under their care. K. Cummings (Illinois Natural History Survey), J. Landye, and W. Miller (University of Arizona) generously donated specimens and notes.

Scanning electron micrographs were taken by Susann Braden of the NMNH (USNM) Scanning Electron Microscopy Laboratory, and prints of these were made by Victor Krantz, and staff of the NMNH Office of Printing and Photographic Services. Shell drawings and drainage map were prepared by M. Ryan (NMNH, Invertebrate Zoology); S. Escher inked anatomical drawings. Collecting permits were provided by Department of Fish and Game (State of California). Partial support for fieldwork and laboratory studies was provided by contracts issued to the author by Department of Fish and Game (State of California), and California Department of Parks and Recreation. Assistance with fieldwork was provided by S. Ellis (California Department of Fish and Game), J. Kerbavaz (California Department of Parks and Recreation), and D.

Sada. I thank Barry Roth and an anonymous reviewer for comments on the manuscript.

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BOOKS, PERIODICALS & PAMPHLETS

Bulimulidae: Catalog of Species

by C. LEONARD RICHARDSON. 1995. *Tryonia* No. 28. 458 pp. \$60.00.

Characteristic of the modern practice of malacology is a global demand for taxonomic authority files—those documents and databases that reflect state-of-the-art opinions on the valid names of taxa, synonyms, authorship, and classification. Indeed, it is hard to imagine natural heritage programs or museum departments running effectively without them. As more and more agencies worldwide become concerned with biodiversity record-keeping, it becomes ever more important to inspect new publications that might be used as the basis for authority files and hence affect the course of future administrative decisions.

Tryonia is a data-rich series published on an occasional basis by the Department of Malacology of the Academy of Natural Sciences of Philadelphia. Its volumes focus on research resources of that department and other malacological information resources. Previous volumes by Leonard Richardson that catalogue species in the families of land snails include Nos. 3 (Helicidae), 6 (Helminthoglyptidae), 9 (Bradybaenidae), 10 (Oreohelicidae), 12 (Camaenidae), 13 (Polygyracea), 16 and 18 (Streptaxacea, parts 1 and 2), 19 (Partulidae), 22 (Urocoptidae), 25 (Cerionidae), and 27 (Bulimulacea: Amphibulimidae, Anadromidae, Grangerellidae, Odontostomidae, Orthalicidae).

Genera of the Bulimulidae are presented in alphabetical order; species are arranged alphabetically under a genus, and each species-name is followed by a list—a long list in many cases—of literature citations of that name. A typical page averages about 62 such citations. Over the length of the volume this calculates to over 24,300 citations, a tribute to the diligence of compiler Richardson.

The lists of citations are not formal synonymies. They simply present references in the literature to a species-name, whether or not the reference work treated it as valid. They do not record the genus-names used in any of the citations. However, since the primary catalogued entities are *taxa* (that is, they are regarded as valid species, with synonyms cited, and assigned to specific genera), the catalogue is a kind of hybrid, and careless users run the risk of confusing taxa with names.

I would have liked very much to be able to report that this work succeeds as a record of the state of the art of bulimulid systematics. It was therefore disquieting to find that in about 3 minutes at my computer, logged on to a widely accessible biological literature database, I was able to locate 17 articles on Bulimulidae not listed by Richardson, including five that propose new taxa, another that

assigns to Bulimulidae two taxa formerly in another family, five that make other significant taxonomic changes (backed up by creditable data and argument), and five that present important geographic reviews.

In *Rabdotus* Albers, 1850, a taxon with which I have some experience, only three species have any references later than Breure (1979), and two of those citations come from one paper. The curtain seems to fall at 1984. Absent are Hoffman (1987) with the description of *Rabdotus milleri*; Hoffman (1988) with its reassignment of 20 species from *Rabdotus* to *Naesiotus*; Smith et al. (1990) with complete locality records for the taxa of Baja California and a new species (of the subgenus *Plicolumna*, wrongly synonymized under *Bulimulus* by Richardson); and Roth & Megaw (1989) with description of the geologically earliest occurrence of *Rabdotus*. All of these references are from the mainstream literature; at least the last two were sent as separates to the Department of Malacology in connection with its commendable reprint exchange program. Why did Richardson not cite them?

Rabdotus nigromontanus (properly a species of *Naesiotus* according to Hoffman, 1988) appears to be catalogued as a synonym of *Rabdotus dealbatus*, although none of the cited references treats it as such. Or perhaps that is not what Richardson means; according to the introduction, the “+” sign as used before the name *nigromontanus* designates names “that have been associated with a species (i.e., synonyms, varieties, subspecies, etc.).” Such a loosely defined convention tells the user little about the real status of the name or taxon. More disturbing is the possibility that because *Naesiotus nigromontanus*, actually a valid species with a limited range in southern Arizona, is not given full standing in this catalogue, it will be mis-curved in research collections, left out of biogeographic studies, or excluded from natural heritage databases.

These are merely sample criticisms, about taxa known to me. Further limitations of this work are those of the printed catalogue medium in general. The editor-in-chief of *Tryonia*, Gary Rosenberg, has recently written (Rosenberg, 1993:257), “The electronic database represents the next step in the production of such catalogues. . . . Printed catalogues are static, whereas databases are dynamic. Information in a database can be reorganized (alphabetically, systematically, geographically, chronologically, etc.) to suit the needs of the user. It can be queried in numerous ways, limited only by the ingenuity of the researcher and the types of raw data utilized by the database.” He might also have added that the best current opinion can be continually patched in, group by group, constantly enhancing the resource. It is too bad that the data in “Bulimulidae: Catalog of Species” did not first appear in dynamic, publicly accessible database form, rather than being locked—errors

and all—into this more static, almost anachronistic, document form.

B. Roth

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The Veliger 38(4):375 (October 2, 1995)

THE VELIGER

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NOTES, INFORMATION & NEWS

International Commission on Zoological Nomenclature

The following applications were published on 30 March 1995 in Volume 52, Part 1 of the *Bulletin of Zoological Nomenclature*. Comment or advice on these applications is invited for publication in the *Bulletin* and should be sent to the Executive Secretary, I.C.Z.N., % The Natural History Museum, Cromwell Road, London SW7 5BD, U.K.

Case 2949—*Aplysia juliana* Quoy & Gaimard, 1832 (Mollusca, Gastropoda): proposed conservation of the specific name.

Case 2922—*Octopus vulgaris* Cuvier, [1797] and *Loligo vulgaris* Lamarck, 1798 (Mollusca, Cephalopoda): proposed conservation of the specific names.

The following Opinions concerning mollusks were published on 30 March 1995 in Volume 52, Part 1 of the *Bulletin of Zoological Nomenclature*. Copies of these Opinions can be obtained free of charge from the Executive Secretary at the address given above.

Opinion 1791. *Pleurotoma meneghinii* Mayer, 1868 (currently *Asthenotoma meneghinii*; Mollusca, Gastropoda): neotype replaced by rediscovered lectotype.

Opinion 1793. *Chtenopteryx* Appellöf, 1890 (Mollusca, Cephalopoda): confirmed as the correct original spelling.

Manuscript Reviewers for Volume 38 of The Veliger

The following outside reviewers contributed their time and effort to evaluate manuscripts submitted during the course

of production of Volume 38. The quality of *The Veliger* depends strongly on the voluntary service of independent reviewers such as these, and we are grateful to all of them.

J. A. Allen, W. D. Allmon, N. Babrakzai, H. Bertsch, A. G. Beu, J. S. Bleakney, P. Bouchet, G. M. Branch, R. C. Bullock, J. T. Carlton, M. R. Carriker, J. G. Carter, H. W. Chaney, K. B. Clark, E. V. Coan, M. J. Collins, R. H. Cowie, C. N. D'Asaro, R. T. Dillon, Jr., D. J. Eernisse, W. K. Emerson, N. J. Evans, H. L. Fairbanks, D. W. Foltz, P. W. Frank, C. G. Franz, T. J. Frest, B. Fried, J. Geller, F. Giusti, C. M. Givens, T. R. Gosliner, R. P. Guralnick, R. T. Hanlon, M. G. Harasewych, M. E. Harte, J. H. Hartman, J. M. Healy, C. O. Hermans, R. Hershler, C. S. Hickman, K. E. Hoagland, F. G. Hochberg, M. Jackiewicz, D. S. Jones, P. Jung, A. R. Kabat, G. L. Kennedy, A. J. Kohn, A. Kress, J. G. J. Kuiper, N. H. Landman, D. R. Lindberg, C. C. Lu, W. G. Lyons, G. L. Mackie, L. N. Marinovich, B. A. Marshall, J. H. McLean, P. S. Mikkelsen, S. V. Millen, W. B. Miller, E. J. Moore, B. Morton, D. K. Padilla, L. R. Page, G. Paulay, T. A. Pearce, C. H. Peterson, W. F. Ponder, R. S. Prezant, T. A. Rawlings, R. L. Reeder, D. G. Reid, P. D. Reynolds, B. R. Rivest, L. L. Robbins, R. Robertson, P. U. Rodda, S. H. Rogers, D. Rollinson, M. P. Russell, A. S. M. Saleuddin, L. R. Saul, W. B. Saunders, P. H. Scott, G. A. Skilleter, R. L. Squires, R. R. Strathmann, J. T. Sullivan, M. J. S. Tevesz, C. Thiriot-Quievreux, K. A. Thomas, F. G. Thompson, C. D. Trowbridge, J. W. Tunnell, Jr., M. Vecchione, G. J. Vermeij, J. Voltzow, N. A. Voss, H. W. Waldén, T. R. Waller, M. W. Yipp, T. P. Yoshino.

Manuscripts

Manuscripts must be typed, one side only, on A4 or equivalent (e.g., 8½" × 11") white paper, and double-spaced throughout, including references, figure legends, footnotes, and tables. All margins should be at least 25 mm wide. Text should be ragged right (i.e., not full justified). Avoid hyphenating words at the right margin. Manuscripts, including figures, should be submitted in triplicate. The first mention in the text of the scientific name of a species should be accompanied by the taxonomic authority, including the year, if possible. Underline scientific names and other words to be printed in italics; no other manipulation of type faces is necessary on the manuscript. Metric and Celsius units are to be used. For aspects of style not addressed here, please see a recent issue of the journal.

The Veliger publishes in English only. Authors whose first language is not English should seek the assistance of a colleague who is fluent in English before submitting a manuscript.

In most cases, the parts of a manuscript should be as follows: title page, abstract, introduction, materials and methods, results, discussion, acknowledgments, literature cited, figure legends, footnotes, tables, and figures. The title page should be a separate sheet and should include the title, authors' names, and addresses. The abstract should be less than 200 words long and should describe concisely the scope, main results, and conclusions of the paper. It should not include references.

Literature cited

References in the text should be given by the name of the author(s) followed by the date of publication: for one author (Phillips, 1981), for two authors (Phillips & Smith, 1982), and for more than two (Phillips et al., 1983). The reference need not be cited when author and date are given only as authority for a taxonomic name.

The "literature cited" section should include all (and only) references cited in the text, listed in alphabetical order by author. Each citation must be complete, with all journal titles *unabbreviated*, and in the following forms:

a) Periodicals:

Hickman, C. S. 1992. Reproduction and development of trochacean gastropods. *The Veliger* 35:245–272.

b) Books:

Bequaert, J. C. & W. B. Miller. 1973. *The Mollusks of the Arid Southwest*. University of Arizona Press: Tucson. xvi + 271 pp.

c) Composite works:

Feder, H. M. 1980. Asteroidea: the sea stars. Pp. 117–135 in R. H. Morris, D. P. Abbott & E. C. Haderlie (eds.), *Intertidal Invertebrates of California*. Stanford University Press: Stanford, Calif.

Tables

Tables must be numbered and each typed on a separate sheet. Each table should be headed by a brief legend. Avoid vertical rules.

Figures and plates

Figures must be carefully prepared and submitted ready for publication. Each should have a short legend, listed on a sheet following the literature cited. Text figures should be in black ink and completely lettered. Keep in mind page format and column size when designing figures. Photo-

graphs for halftone reproduction must be of good quality, trimmed squarely, grouped as appropriate, and mounted on suitably heavy board. Where appropriate, a scale bar may be used in the photograph; otherwise, the specimen size should be given in the figure legend. Photographs should be submitted in the desired final size.

Clear xerographic copies of figures are suitable for reviewers' copies of submitted manuscripts. It is the author's responsibility to ensure that lettering will be legible after any necessary reduction and that lettering size is appropriate to the figure.

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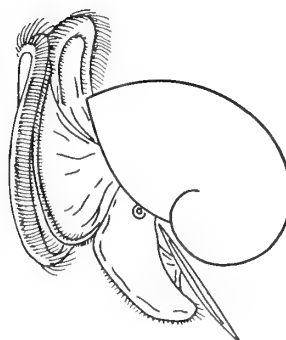
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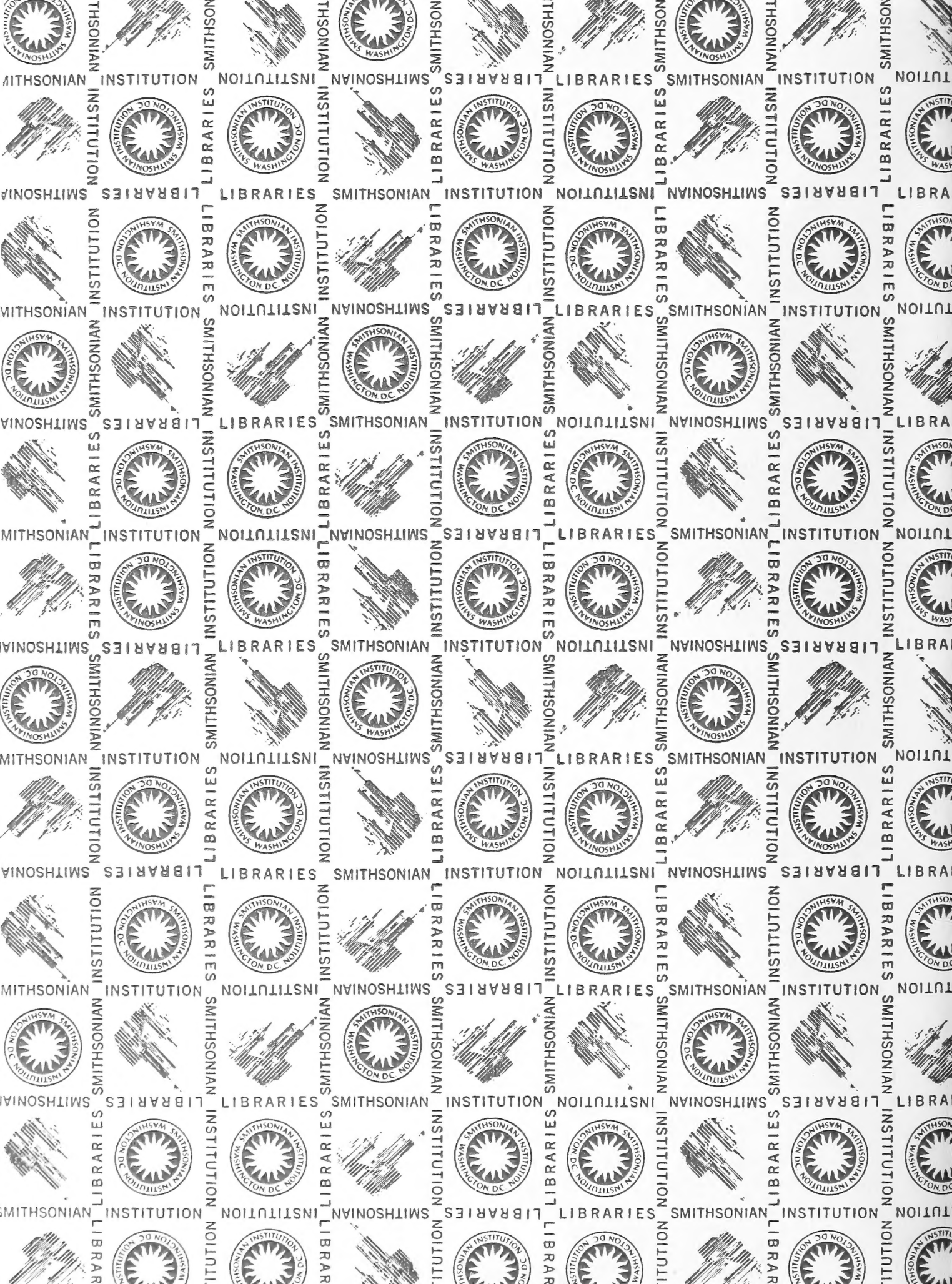
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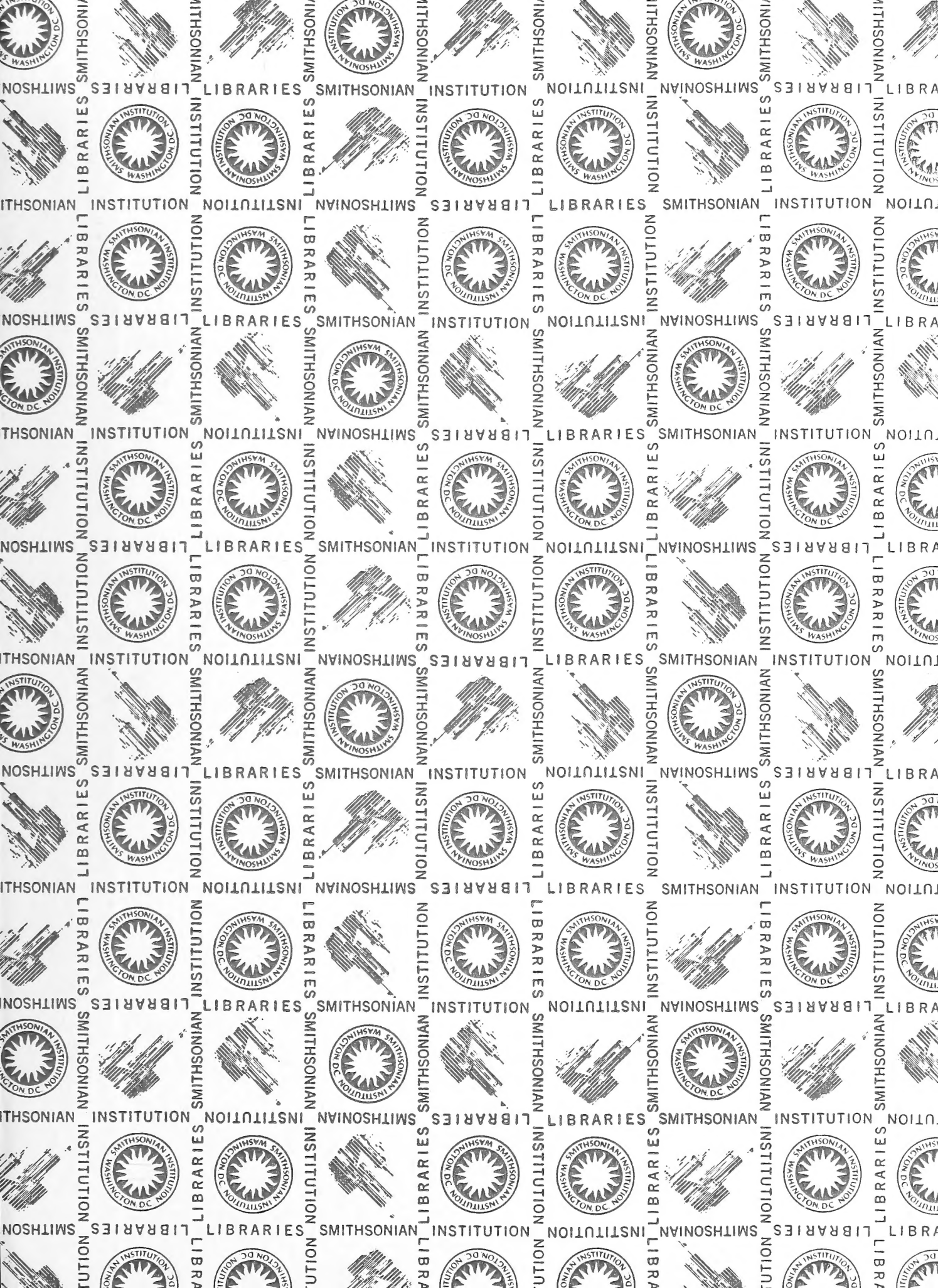
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